INTRA- AND INTER-SPECIFIC COMPETITION AMONG JUVENILE ATLANTIC SALMON (*Salmo salar* L.) AND BROWN TROUT (*Salmo trutta* L.)

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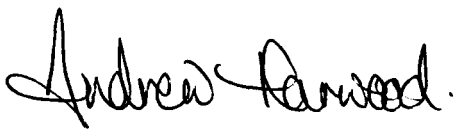
Declaration

I declare that the work described in this thesis has been carried out by myself unless otherwise cited or acknowledged. It is entirely of my own composition and has not, in whole or in part, been submitted for any other degree.



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To my parents:

For their love, support and encouragement.

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SUMMARY

The main aim of this thesis was to study intra- and inter-specific competition among juvenile Atlantic salmon and brown trout. The study concentrated on two critical times for survival: first, the period from shortly after emergence until later in the summer when individuals first establish territories; and second, during the winter, when many salmonid populations experience a bottleneck. In addition, the stability of social hierarchies and the influence these have on growth and survival were studied on older individuals in the summer. Experiments were carried out in a variety of conditions ranging from small arenas and artificial stream channels where behavioural interactions among fish could be observed, to the wild where it was possible to test inferences derived from laboratory observations in an ecological context.

Both salmon and trout are known to undergo a behavioural shift in winter, switching from being primarily diurnal during the summer to being predominantly nocturnal in winter. Atlantic salmon and brown trout forage in slow-flowing water at night and shelter in interstitial spaces in the substrate during the day. This thesis shows that salmon and trout compete for both foraging (chapter 2) and sheltering (chapter 3) habitat in winter, illustrating that competition between the two species is not restricted to the summer months. Trout were shown to dominate salmon in competition for foraging habitat, forcing them to move into shallower water or become more diurnal (chapter 2). Intra- and inter-specific competition for shelters was equal in intensity and more dependent on arrival time (prior residency) than species identity (chapter 3).

This competition could have short- and long-term survival consequences for over-wintering fish, particularly Atlantic salmon, and have implications for the carrying capacity of streams.

Intrinsic dominance status and prior residence advantage were both shown to influence the feeding rate and amount of time spent in good quality feeding sites of Atlantic salmon fry (chapter 4). The two factors were approximately equal in strength, although there was some evidence that dominance may eventually override a prior residence advantage. These findings have implications for the emergence times of salmon fry as early arrival may offset intrinsic disadvantages in aggressiveness or size. However, the influence of prior residence on feeding success was shown to be variable and dependent on the nature of the resource (chapter 5). Although food resources were unpredictable in time in both chapters 4 and 5, those in chapter 5 were more spatially unpredictable and fry in this experiment gained no prior residence advantage. This therefore confirms previous work in which a resident's dominance advantage is expressed to a greater degree when the value of the resource is high. Comparisons of chapters 4 and 5 also suggest that the density of fish, and therefore the intensity of competition, may also play an important role in determining how contests are resolved.

The formation of within-species dominance hierarchies was influenced by inter-specific interactions, with size being positively correlated with feeding success in allopatric but not sympatric groups (chapter 6). In contrast, the rate of aggression was correlated to feeding success in both allopatry and sympatry.

These results suggest that the advantages of social dominance may be specific to the species assemblage. Chapter 6 also illustrates the methods by which resources can be partitioned as subordinate trout fed at different times to dominant trout, and salmon in sympatry were able to adopt an alternative behavioural strategy that allowed them to continue feeding in the presence of more aggressive trout.

Chapter 7 provides a cautionary note that although dominance may provide growth benefits in the laboratory these are not necessarily applicable in the wild. Salmon that dominated other individuals and monopolised point sources of food in the laboratory showed no growth benefits over a two-month period in their natural stream. This is likely to be due to a combination of factors such as resource variability, sympatric interactions, disturbance and predation.

This thesis has provided detailed behavioural observations of competition among Atlantic salmon and brown trout and has shown the importance of resource variability, species assemblage, season and environment on the resolution of conflicts. Testing these findings in conditions more closely matching those in natural streams is the next obvious step in assessing the importance of competition among salmonids.

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Brown trout in an artificial stream

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Competition is understandably widespread in the natural world, with the limited availability of resources such as access to food and water restricting the size populations can reach (Moynihan 1998). Furthermore, the list of resources for which animals compete is extensive, ranging from daily requirements such as food, air or places in which to hide from predators, to seasonal resources such as breeding sites and reproductive partners. Competition is also not restricted to animals, with plants competing for resources such as light, minerals and water (e.g. Schulz 1960). Competition is therefore ubiquitous. Despite this, the influence of competition has been the subject of much debate, largely because of the more subtle effects it has on populations compared to, for instance, predation (e.g. Connell 1983; Schoener 1983; reviewed in Ricklefs 1990). Nevertheless, competition has played an important role in ecological theories ever since Darwin based his theory of evolution on the expression of competition between individuals of the same species. Such intra-specific competition can lead to density dependence of birth and death rates and thus potentially regulates the size of a population within parameters imposed by the environment (Ricklefs 1990). This concept of density dependence is of fundamental importance to population biology and has widespread implications for ecology and conservation (Krebs & Davies 1997). For instance, if conservationists wish to decrease the impact of exploitation on an endangered species by reducing mortality caused by predators, disease or habitat loss, then it is usually necessary to understand the role density

dependence plays in population regulation. When members of different species compete (inter-specific competition) the population density of one can influence the birth and death rates of the other. Therefore, either through direct interference (interference competition) or the depletion of mutual resources (exploitative competition; see Park 1962), competition between species can affect their population dynamics and densities at carrying capacities (i.e. maximum number of individuals in a habitat) (Ricklefs 1990).

Competition often leads to the formation of social hierarchies whereby dominant individuals are able to gain preferential access to (or even monopolise) resources at the expense of subordinates. Such hierarchies appear throughout the animal kingdom from social insects through to primates (Wilson 1975). Atlantic salmon and brown trout (see Appendix 1 for scientific names) are two species that show similar ecological requirements and geographical distributions and are known to compete for food and habitat in the wild (e.g. Kennedy & Strange 1986a,b). Furthermore, wild stocks of both species have been dwindling and competition between the species may therefore have important management implications. The objective of this thesis is to investigate intra- and inter-specific competition among juvenile Atlantic salmon and brown trout, and to determine the role dominance hierarchies play in this competition. Whilst there have been many studies of social interactions within species of salmonid, this thesis is among the first to attain detailed behavioural observations of the interactions between species and of intra-specific competition amongst Atlantic salmon fry. This chapter introduces the basic concepts of social hierarchies and intra- and inter-

specific competition; summarises the biology of Atlantic salmon and brown trout, and provides an overview of the content of the thesis.

1.2 Intra-specific competition and dominance hierarchies

The majority of studies concerned with social hierarchies have concentrated on relationships between individuals of the same species, and these have revealed the variety of forms that hierarchies can take, as well as the variable means by which hierarchies are formed and maintained (reviewed in Wilson 1975). The simplest form of hierarchy is where one individual, a despot, dominates all other individuals. The best example of this is the social insects, such as the paper wasps, in which a single female, the queen, physically dominates the remainder of the colony. In the more advanced insect societies, such as ants and termites, the queen maintains her superior status not through overt aggression but through the use of pheromones which inhibit the reproductive behaviour and development of immature members of the colony.

The most common form of hierarchy is a linear sequence where an alpha individual dominates all others, a beta individual dominates all but the alpha, and so on through a group of individuals. Non-linear hierarchies also exist in which there may be circular elements in an otherwise linear chain. However, these have often been found to be early or disruptive stages in the formation of a dominance hierarchy that are later replaced by a linear hierarchy (e.g. Murchison 1935; Tordoff 1954), although this is not always the case (e.g. Moolman et al. 1998).

Dominance hierarchies are distributed throughout the animal kingdom from crustaceans (e.g. red swamp crayfish, Figler et al. 1999), to amphibians (e.g. dart-poison frog; Baugh & Forester 1994), birds (e.g. willow tit, Koivula et al. 1993), rodents (e.g. highveld mole-rat, Moolman et al. 1998), and many other mammalian species. Dominance relationships are also widespread among species of fish including cichlids (e.g. freshwater angelfish, Chellappa et al. 1999), poeciliids (e.g. green swordtail fish, Beaugrand et al. 1991) and salmonids (e.g. Arctic grayling, Hughes 1992). The means by which these hierarchies are established and maintained vary considerably, and can range from obvious physical factors such as size and age, to chemical cues such as pheromones, and historical factors such as prior residence or length of time spent within the group (see Wilson 1975). The most influential factors involved in predicting dominance in groups of salmonid fish are size, aggressiveness, and prior residence, all of which are discussed in greater detail in later chapters.

1.3 Inter-specific competition

The importance of intra-specific competition and social hierarchies is evident from their widespread distribution throughout the natural world. However, no species exists in isolation. Inter-specific competition, therefore, is also of general importance in ecology. Lotka and Volterra proposed the first theoretical model to explain the influence of inter-specific competition on population processes (reviewed in Ricklefs 1990). Their logistic model and experimental work by Gause (1932) led to the development of the competitive exclusion principle (a phrase first used by Hardin (1960) but previously discussed under the names of

its principle authors: Volterra and Gause) which states that two species cannot coexist on a single limiting resource. Tilman (1982) represented competition between two species in a different manner by plotting graphs relating population change to resource availability. However, both these portrayals of inter-specific competition arrive at the same conclusion: ecological segregation allows two species to coexist. Ecological segregation, or the partitioning of available resources, is therefore widespread and has been reviewed by Schoener (1974) for primarily mammals and birds, and by Ross (1986) for fishes. The partitioning of resources between members of the same and different species is also discussed in greater detail in later chapters.

Early experiments on inter-specific competition in the laboratory (Park 1954, 1962) and in the field (Connell 1961) demonstrated that the relative performance of the two species under different environmental conditions was critical in determining the outcome of competition and the geographical range of each species. Connell (1961) demonstrated that the distribution of Poli's stellate barnacle within the intertidal zone was dependent not on physiological tolerance limits, but on the distribution of adult members of an acorn barnacle species. As with many early experiments concerned with inter-specific competition, the results were based on the response of one species to the removal or addition of individuals of the other species. Although such experiments suggest the existence of inter-specific competition, they do not allow an assessment of the relative magnitudes of intra- and inter-specific competition because the density of animals between the experimental and control treatments are different. To overcome this problem de Wit (1960) developed the substitution experiment in

which the total density of individuals remains constant while the ratio of individuals of the two species varies. Ricklefs (1990) and Fausch (1998) discuss the advantages and disadvantages of these methods of studying intra- and inter-specific competition. Throughout this thesis, the substitution method is used in order that the relative strengths of intra- and inter-specific competition can be assessed.

Inter-specific competition can have wide-ranging effects, from increasing the productivity of commercially valuable trees by removing species of little economic importance (Schulz 1960), to explaining geographical variation in blue tit song due to song divergence in the presence of great tits (Doutrelant & Lambrechts 2001). The importance of inter-specific competition in character displacement has recently been shown in threespine sticklebacks in which the strength of competition between coexisting species declined as character divergence increased (Pritchard & Schluter 2001). Competitive interactions, both within and between species, are also important in determining the responses of species and communities to environmental change (Davis et al. 1998a,b; Navas 1998; but see Fox & Morin 2001), and may thus become of increasing importance when considering man's impact on the natural world.

1.4 Biology of Atlantic salmon and brown trout

In many aspects, the lives of Atlantic salmon and brown trout are inseparable. The two species, both cold water fish belonging to the family Salmonidae, share many similarities among their life-history strategies, diet and choices of habitat

(Giles, 1994; Heggenes et al. 1999). The similarities are not only restricted to their ecology; their geographical distribution shows a great deal of overlap as well. The natural marine range of the Atlantic salmon is the north Atlantic ocean, with the freshwater stages living in streams and rivers on both sides of the Atlantic. Its distribution extends northwards to Iceland and Greenland and southwards to northern Portugal and Connecticut (Jones 1959). Recent introductions and releases of cultured fish have extended its range to include Argentina, Australia, Chile and New Zealand. The natural range of brown trout runs from Iceland to Afghanistan with North Africa's Atlas mountains having the most southerly natural population. Widespread introductions have taken brown trout to the United States, Canada, South America, Australia, New Zealand, Africa and India (Giles 1994). Such parity in ecology and distribution invariably leads to competition.

For both species, life begins in a gravel redd in fresh water. A redd is a series of excavations (nests) which an adult female cuts by swimming on her side and using her caudal fin like a paddle. Once a nest is excavated, the male aligns himself beside her and eggs and milt are released, after which the female covers them in gravel (Scott & Crossman 1973; Giles 1994). The eggs hatch approximately 100 days later and the young alevins spend a variable period within the redd while obtaining nourishment from their yolk sac (Dill 1977). Once their yolk sac is exhausted (usually in mid spring), young fry emerge from the gravel and commence 'swim-up' behaviour under the cover of darkness (Brännäs 1987), a process which allows them to fill up their swim bladder and obtain neutral buoyancy (Kalleberg 1958). The young fry swim with noticeable

difficulty until the swim bladder is filled, either by collecting air from the water surface or swallowing air bubbles in the water column. Neutral buoyancy is usually obtained within a week (Dill 1977) after which feeding and territorial behaviour begin (Elliott 1986).

At this stage in the life cycle, the fish usually become territorial, aggressively defending small feeding stations which they constantly patrol (Kalleberg 1958). In this way some individuals become excluded from the best feeding positions and these are often forced to migrate away from the vicinity of the redd to search for more available habitat (Elliott 1990). This frequently leads to high mortality rates amongst the fry, especially when the density is high, with many fry starving to death due to intense competition for feeding territories. Indeed, the period between hatching and the establishment of feeding territories is the phase of highest mortality in the life-cycle of both salmon and trout, with both starvation and predation playing a role (Peterman & Gatto 1978; Elliott 1989; Giles 1994). These early juvenile mortalities are thought to be density dependent (Mortensen 1977a,b; Elliott 1986) and this early limit on salmonid population densities can define a stream's carrying capacity (Egglishaw & Shackley 1977, 1980; Elliott 1985a,b; Heggenes et al. 1999).

The territories of salmon and trout are formed around a centrally located spot, called the primary station, which is the point from which the majority of feeding and aggressive acts originate (Keeley & Grant 1995). Both salmon and trout are sit-and-wait predators that emerge from their primary station to intercept drifting invertebrates (Stradmeyer & Thorpe 1987), predominantly the larvae of mayflies,

stoneflies, caddisflies and chironomids (Giles 1994). The optimal position for a primary station is in an area of low water velocity to minimise the energy expended on swimming, yet close to swift currents to maximise access to invertebrate drift (Fausch & White 1981; Fausch 1984). Although the majority of juvenile salmonids adopt a territorial drift feeding strategy, a small number of individuals adopt a more mobile strategy feeding on benthic invertebrates rather than those drifting in the water column (e.g. Grant & Noakes 1987; Armstrong et al. 1999; Nakano et al. 1999). Under certain conditions, such as when water velocity is low within pools, fish may also form loose hierarchies rather than the more common territorial mosaic (Kalleberg 1958).

The acquisition of a suitable feeding site is often essential to survival and early emergence could therefore prove advantageous. Several studies have indeed shown that fry emerging early to colonise the stream-bed have an advantage in subsequent competition for feeding sites over those emerging later (Mason & Chapman 1965; Chandler & Bjornn 1988). This could be because they have a 'prior residence' advantage and/or because they are intrinsically more dominant. However, the advantage of emerging early from the redd could be counteracted by the increased chance of being eaten, and Gustafson-Marjanen & Dowse (1983) found that almost all fry emerged in a three night period. The risk of failing to compete effectively for limited territorial space also makes late emergence hazardous, thus favouring synchronous emergence (Brännäs 1995).

Those fry that survive the first two months of life to become parr continue to feed during the summer months. It is here that the life-history strategies of

salmon and trout diverge. The majority of Atlantic salmon transform into smolts and undergo a seaward migration at some point during the course of their lives, whereas many trout, called brown trout, spend their entire lives in fresh water (Giles 1994). Other subspecies of trout either undergo a migration to estuaries ('slob' trout), whereas yet others (sea trout) smoltify and undergo a full sea migration, as in the Atlantic salmon.

The growth rates of Atlantic salmon parr between April and July determine whether they will smolt during their first year, thus becoming S1 fish, or delay smoltification, and thus migration, for at least another year (S2 fish; Thorpe 1977). The decision to smolt is therefore dependent on growth rate, which is influenced by environmental factors, such as day length and temperature that determine feeding opportunity, and social interactions that determine whether the fish take that opportunity (Metcalfe et al. 1990a). Those that will migrate in the spring undergo a surge in appetite in the autumn and they continue to feed throughout the winter, whereas delayed migrants show a progressive loss of appetite until by early winter their intake is negligible (Metcalfe et al. 1986; Metcalfe & Thorpe 1992). Thus a bimodal size distribution can arise within a population of salmon fry, with fish belonging either to the upper modal group (S1 fish) or the lower modal group (S2 fish; see Thorpe 1977). This distribution remains stable through until smolting unless there is a major change in environmental conditions (Metcalfe 1994). The age at which Atlantic salmon undertake seaward migration varies between one and eight years and they may spend between one and six years at sea before returning to spawn. Much of this variation is dependent on environmental conditions (Thorpe 1989; Metcalfe &

Thorpe 1990), although genetics may also play some role in determining the life history and growth patterns of individual fish (Giles 1994).

1.4.1 Daily and seasonal variation in behaviour

Juvenile salmonids switch from being active during day and night for most of the year to being nocturnal during the winter months (Fraser et al. 1993, 1995; Heggenes et al. 1993, 1999). The function of this change in daily activity rhythm in which salmonids seek shelter during the day (Cunjak 1988; Heggenes & Saltveit 1990) is thought to be primarily to hide from diurnal predators (Valdimarsson & Metcalfe 1998). However, the switch to nocturnal activity may also be a strategem for avoiding being trapped by anchor ice (Heggenes et al. 1993; Whalen et al. 1999) or may be a response to the pattern of drifting or benthic invertebrates (e.g. Amundsen et al. 2000). The cost of such a strategy is decreased feeding efficiency, for salmonids are visual foragers (Stradmeyer & Thorpe 1987) and even on the brightest nights Atlantic salmon feed at only 35% of their daytime efficiency (Fraser & Metcalfe 1997). The shift from diurnal to nocturnal activity is driven predominantly by water temperature (Fraser et al. 1993; Valdimarsson et al. 1997), with low summer temperatures also causing salmon to become nocturnal (Fraser et al. 1995).

The decision on when to feed during a 24 hour period is also dependent on the life-history strategy adopted by individuals and their current state (Metcalfe et al. 1998). Metcalfe et al. (1998) found that fish with a greater need for growth, that is those that would migrate in spring, were willing to risk the increased predation

risk and feed during the day. Nicieza & Braña (1993) also found that the extent of late winter growth in salmon preparing to migrate was strongly and negatively correlated with their body size at the onset of winter. In addition, wild fish have been shown to have size (Gries et al. 1997) and state-dependent (Bradford & Higgins 2001) diel activity schedules. Food intake and growth have previously been attributed to water temperature and fish size; however, the light-dark cycle also has a role to play as it provides a frame for visual feeding and an indicator of time of day and season (Eriksson & Alanärä 1990).

Salmonids active during the night have been shown to prefer slower water currents in which prey items can be more readily seen (Heggenes et al. 1993; Mäki-Petäys et al. 1997; Metcalfe et al. 1997). Large substrates are also preferred in winter as they provide better shelter (Rimmer et al. 1984; Cunjak 1988).

1.5 Aims and objectives

This thesis concentrates on intra- and inter-specific competition between Atlantic salmon and brown trout, particularly during winter, which can be a population bottleneck for salmonids (Bjornn 1971; Mason 1976), and after emergence when mortality is at its peak (Elliott 1989; Cunjak et al. 1998). This work has important implications for the conservation and management of both species as many salmonid populations are in decline and juvenile fish are commonly stocked into rivers worldwide in order to increase the productivities of streams (Cowx 1994). The social interactions between them, particularly at natural

bottlenecks in population size, may therefore influence stocking and management strategies. The variation in daily and seasonal behaviour may also have implications for aquaculture. An increased understanding of behavioural patterns may increase productivity by allowing feeding regimes and housing conditions to be adjusted to suit the natural behaviour of fish.

In chapter 2, I examine the habitat requirements of Atlantic salmon and brown trout whilst they are active at night during the winter, and the spatial and temporal effects of inter-specific competition. Intra- and inter-specific competition for shelters during the day in winter, both when shelters are provided in excess and when limited, is then investigated in chapter 3. In chapter 4, I explore the relative influence of prior residence and dominance on territory acquisition in Atlantic salmon fry. The ability to retain a territory, and the effect that prior residence has on this ability, is then studied in chapter 5. In chapter 6, I study the formation of dominance hierarchies in single- and mixed-species groups of Atlantic salmon and brown trout to determine whether the same factors influence dominance status under different social conditions. In chapter 7, I examine whether the dominance status of Atlantic salmon evident under laboratory conditions is transferred into higher growth and survival rates in the wild. Finally, chapter 8 is a general discussion, bringing together results and ideas generated by this thesis with reference to other relevant work.

CHAPTER 2: SPATIAL AND TEMPORAL EFFECTS OF INTER-SPECIFIC COMPETITION BETWEEN ATLANTIC SALMON AND BROWN TROUT IN WINTER

2.1 Abstract

Previous work has shown that juvenile stream-dwelling salmonids become predominantly nocturnal during winter by emerging from daytime refuges to feed, with several species having been shown to prefer slow-flowing water whilst active at night. I used semi-natural stream channels, landscaped to provide a choice of water depths and hence velocities, to test whether Atlantic salmon and brown trout show similar habitat preferences during winter. I also tested whether there was any spatial or temporal displacement of Atlantic salmon when in sympatry with brown trout. Night-time observations revealed that Atlantic salmon did have a preference for slow-flowing water. However, when in direct competition with trout, salmon either remained predominantly nocturnal but occupied shallower water, or became significantly less nocturnal, spending more time active during the day than when in allopatry. These results, which were especially marked in relatively larger fish, indicate that competition between the two species for food and resources is not restricted to the summer months, and may affect both the short- and long-term growth and survival of over-wintering wild Atlantic salmon.

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2.2 Introduction

Diel activity patterns of organisms result from the need to concentrate activity at a time that optimises the balance between competition, predation risk and food availability (Helfman 1993). For instance, individual rainbow trout and Arctic charr may adopt contrasting diel activity patterns, possibly as a result of subordinates attempting to attain adequate growth whilst avoiding high levels of aggression from more dominant fish (Alanärä & Brännäs 1997). A grazing mayfly was aperiodic or weakly nocturnal in a fishless stream, but became more nocturnal when transferred to a trout inhabited stream, illustrating the influence of predation risk on diel feeding (Cowan & Peckarsky 1994).

Both experimental and field studies have shown that juvenile Atlantic salmon undergo a temperature-dependent shift from predominantly diurnal activity above 10 °C to predominantly nocturnal activity at lower temperatures (Fraser et al. 1993, 1995; Bremset 2000). Such a switch may account for seasonal changes in diel activity of not only Atlantic salmon, but also brown trout (Heggenes et al. 1993), rainbow trout (Riehle & Griffith 1993) and Arctic charr (Linnér et al. 1990). This change in behaviour may be a response to their increased vulnerability in winter to diurnal, endothermic predators (Metcalfe et al. 1999) that are not affected by decreased water temperatures, which cause the swimming ability and acceleration of fish to be reduced (Rimmer et al. 1985). Alternatively, the shift to nocturnal activity may be a strategem to avoid being trapped by

anchor ice (Heggenes et al. 1993; Whalen et al. 1999) or may be a response to the pattern of drifting or benthic invertebrates (e.g. Amundsen et al. 2000).

Since salmonids are sit-and-wait predators that rely on vision, the cost of becoming more nocturnal is a decrease in the efficiency of capturing individual food items. Even on the clearest of nights, feeding efficiency is approximately only 35% of that during the day (Fraser & Metcalfe 1997). However, nocturnal foraging may decrease predation risk (expressed per unit of food intake) and therefore may have fitness benefits (Metcalfe et al. 1999). Brown trout prefer slower water currents at night than during the day (Heggenes et al. 1993) presumably in order to see their prey more easily. Moreover, juvenile Atlantic salmon prefer slower water currents on dark nights than on clear nights to facilitate prey capture (Metcalfe et al. 1997). As expected, the preference of salmon to use deep slow water actively on winter nights was observed in the wild by Whalen & Parrish (1999).

A greater use of deep water in winter is likely to cause increased competition for foraging opportunities between sympatric salmon and brown trout. In summer months, juvenile trout are more aggressive than salmon of a similar size (e.g. Kalleberg 1958) and so restrict them to less preferred (i.e. shallower) areas of a stream (Kennedy & Strange 1986b). Such inter-specific competition is thought to have long-lasting effects on growth, survival and fitness (Fausch 1998). Nonetheless, winter has been considered to be the most important period for survival of salmon parr (Cunjak et al. 1998) and inter-specific interactions may

be important at this time of year. However, as yet there is no information on the relative competitive abilities of trout and salmon during winter.

I conducted experiments using artificial stream channels to test three hypotheses:

1. Juvenile Atlantic salmon prefer deep water in winter when living in allopatry (cf. Whalen & Parrish 1999).
2. Juvenile Atlantic salmon are displaced from their preferred habitat when living in sympatry with brown trout.
3. Inter-specific competition for space in winter results in shifts in diel activity patterns and (or) temporal changes in habitat use of juvenile Atlantic salmon.

2.3 Methods

The experiment was conducted in an outdoor artificial stream (previously described in Valdimarsson et al. 1997) at the University Field Station, Rowardennan, Loch Lomondside, Scotland. The stream was 60 cm wide and formed a continuous, approximately oval shaped loop with straight sides. Fish could be observed from within this loop since the inside walls of the channel were made from glass panels. The straight sides of the channel were each six metres in length, however, the variable speed impeller which pumped water around the channel occupied 2.5 m of one side. The remaining straight parts of the channel were partitioned into three 2.25 m experimental arenas using mesh, and landscaped with fine gravel (5-25 mm diameter) to deter fish from hiding in streambed cavities. The gravel was landscaped to produce a smooth gradient

within each arena, with shallow water (10 cm) at the upstream end and relatively deep water (45 cm) at the downstream end. The surface velocity of the water varied continuously from 0.16 m · s^{-1} at the upstream end to 0.03 m · s^{-1} at the downstream end. A 1 m long section between each experimental arena was landscaped with the contrasting gradient in order to decrease turbulence and smooth the flow down the channel. The outer sides of the channel were marked every 15 cm along their length in order to define fifteen zones per arena (zone 1 being at the upstream end) to allow referencing of the recorded positions of the fish. Fish shelters were made from six 1-L opaque bottles that were cut in half lengthwise and embedded in the gravel at regular intervals in each of the experimental arenas, creating cavities in the gravel measuring 17 cm × 8.5 cm × 4.25 cm. These bottles were positioned with the open side against the glass wall to allow any fish within them to be identified, a technique successfully used by Valdimarsson et al. (1997).

Water was pumped constantly from Loch Lomond and ranged in temperature from 4.3-6.1 °C. Light and photoperiod of the outdoor stream channel were the same as ambient conditions of Loch Lomond. However, some overhead cover was provided at all water depths by placing wooden planks approximately 15 cm above the water surface, across half the width of the channel. The position of these planks was randomised with respect to the inside/outside wall of the stream channel. This allowed comparison of the amount of time spent under overhead cover and out of cover. Food was provided by a belt feeder, which dropped pelleted food at a trickle rate at the upstream end of each arena. Fish were

provided with 0.5% of their total body weight in food per day, an amount chosen so that growth would be minimal but fish would not lose condition during the experimental trials. This pelleted food was supplemented by a low level of zooplankton found in the water pumped from Loch Lomond.

Two treatments were used to test the effects of trout on the behaviour of salmon: allopatric (four salmon), and sympatric (two salmon with two trout). Data collected from the salmon in allopatry would reveal whether salmon prefer areas of deep slow-moving water or shallow fast-flowing water, while the sympatric treatment would reveal whether habitat use changes under conditions of inter-specific competition. Fish in both treatments were size-matched to reduce any confounding effects of large size differences. Both treatments were run simultaneously in different arenas of the stream channel to prevent any confounding effects of temperature or time of year influencing the results.

The fish used were wild caught salmon (fork length: mean ± SE = 109.4 ± 1.83 mm; weight = 13.42 ± 0.65 g) and trout (fork length = 100.7 ± 2.77 mm; weight = 9.87 ± 0.90 g) from the River Blane, a tributary of the River Endrick which flows into Loch Lomond. Fish were individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Fish were then allowed to reside in the experimental arenas for a period of 72 hours before observations began.

The observations on each group of fish were then made on four consecutive dates. Each night of observation lasted seven hours and covered the day-night transition at either dusk or dawn. During this observation period the position of each fish was recorded every 30 minutes by scanning briefly with a flashlight, a method thought to minimise the disturbance of the fish (see Heggenes et al. 1993). Data collected during each scan observation consisted of the position of each fish in the water column (either resting on the bottom or swimming in the water column), the number of the zone in which the fish was located (1-15, which was a relative measure of water depth, and hence velocity), and whether or not the fish was under overhead cover. The use of shelters was also recorded to determine the frequency with which fish sought refuge, and light intensity and water temperature were also noted. Light intensity was measured using a Skye Instruments SKL 300 photometer (range 0.01-2000 lx) and recorded as the mean of two measurements made just above the overhead cover provided, in the middle of the straight section on either side of the channel. Light intensity readings were used to split observations into three categories, day ($lx \geq 100$), twilight ($0.02 < lx < 100$) and night ($lx \leq 0.02$). Water temperature was measured using a digital thermometer placed permanently in the stream. After the data for each group were collected, the fish were removed and different fish placed in the test arena. Both treatments were replicated eight times; all fish were used only once. The experiments were carried out between 16th January 1999 and 4th March 1999.

2.3.1 Data analysis and statistical treatment

For the purpose of comparing treatments, the data were split into three categories: salmon in allopatry, salmon in sympatry (with trout) and trout in sympatry (with salmon), with data for the latter two categories coming from the one sympatric treatment. To evaluate the effect of body size on behaviour while standardising for size differences between trials, the relative body length (body length as a proportion of the body length of the largest fish in each group of four fish) was calculated for each fish. All percent data were normalised by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for 2-tailed tests of significance.

Repeated measures analysis of variance (ANOVA) was used to test the null hypothesis that time of day (within-subject effect) and category of fish (between-subject effect) had no effect on response variables (proportion of observations when in refuges, or on substrate or under overhead cover whilst not in refuges).

To compare the timing of activity between treatments the percentage of activity (i.e. time out of shelters) that occurred by night was determined for each fish. This was calculated using the formula:

$$100 \times E_n / (E_n + E_d)$$

where E_n = the % of nighttime and twilight observations during which a fish was out of shelter and E_d = the % of daytime observations during which a fish was out of shelter (Fraser et al. 1995). This was termed the nocturnal index, and ranged from 0 (the fish was only observed out of shelter during the day) to 100 % (it was only observed out at night). In order to compare between treatments a mean value for each category of fish was calculated for each replicate group.

2.4 Results

2.4.1 Time of day effects on the use of cover

As expected, there was a significant difference in the proportion of time that both salmon and trout were observed to spend in refuges during day, twilight and night (Table 2.1, Fig. 2.1). This difference represented a significant decrease in the use of shelters from daytime through twilight to night (linear term of polynomial contrasts: $F_{1,61} = 28.63$, $P < 0.001$). However, there was no significant difference in this time effect between categories of fish (Table 2.1, Fig. 2.1), indicating that both salmon and trout became more active at night. There was a significant difference in the proportion of time that both salmon and trout were observed to spend on the substrate whilst not sheltering during all three time periods (Table 2.1, Fig. 2.2). This difference represented a significant increase in the amount of time spent on the substrate from daytime through twilight to night (linear term of polynomial contrasts: $F_{1,28} = 7.20$, $P = 0.012$). There was also a significant difference between the species, with salmon

Table 2.1. Summary of results from repeated measures ANOVAs testing for the effect of time of day on behavioural responses. In all cases multivariate significance tests were used as Mauchly's test of sphericity was significant.

Source of variation	df	F	P
Proportion of time spent in refuges			
Within-subjects			
Time of day	2,60	16.70	< 0.001
Between-subjects			
Category of fish	2,61	0.74	0.481
Time of day * category of fish	4,122	0.60	0.662
Proportion of time spent on substrate whilst not in refuges			
Within-subjects			
Time of day	2,27	3.70	0.038
Between-subjects			
Category of fish	2,28	8.01	0.002
Time of day * category of fish	4,56	1.93	0.119
Proportion of time spent under overhead cover whilst not in refuges			
Within-subjects			
Time of day	2,27	0.38	0.688
Between-subjects			
Category of fish	2,28	0.60	0.558
Time of day * category of fish	4,56	0.30	0.874

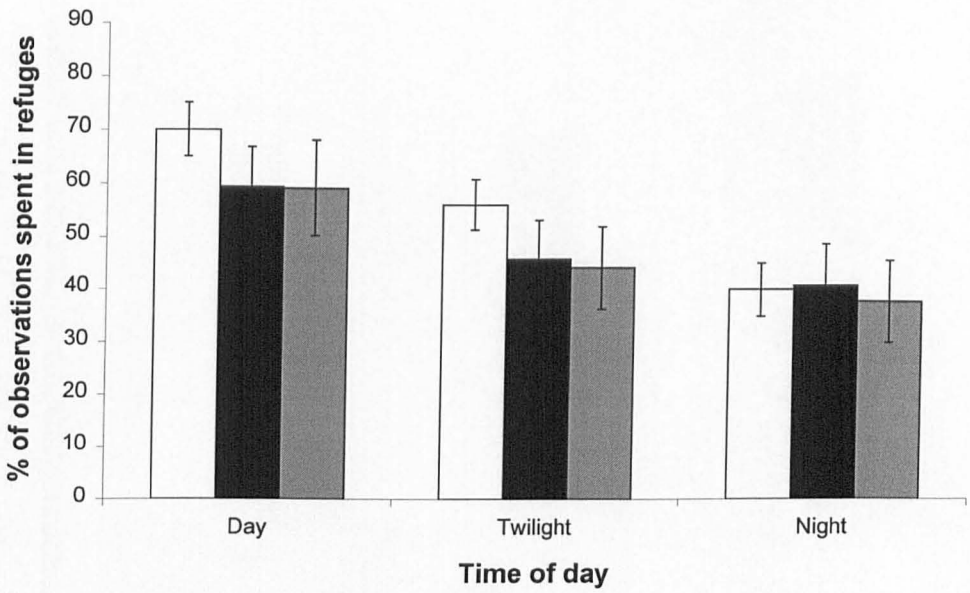

Figure 2.1. Graph of the percentage (±SEM) of observations spent in refuges at various times during a 24 h period for salmon in allopatry (open bars), salmon in sympatry (solid bars) and trout in sympatry (shaded bars). Percentages are arcsine-transformed, thus fish with a value of 90 never left the refuges.

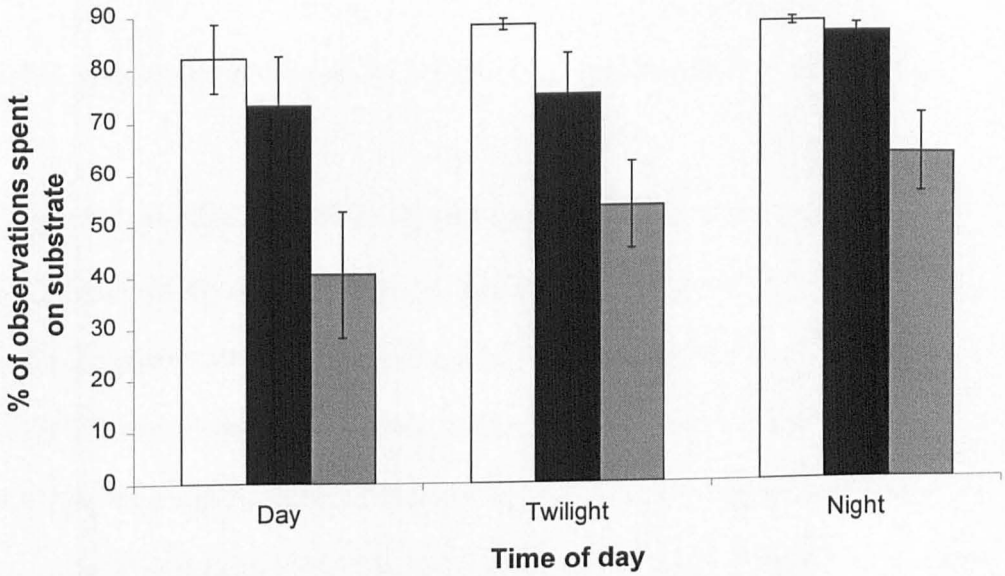

Figure 2.2. Graph of the percentage (±SEM) of observations spent holding position on the substrate whilst not in refuges for salmon in allopatry (open bars), salmon in sympatry (solid bars) and trout in sympatry (shaded bars). Percentages are arcsine-transformed thus fish with a value of 90 were always found resting on the substrate.

observed more often on the substrate than trout (Table 2.1, Fig. 2.2). There was no time of day or species effect on the proportion of time observed under overhead cover (Table 2.1).

2.4.2 Influence of light intensity, temperature and time of year on refuge use

To test for the relative influence of light intensity, time of year (Julian date) and temperature on the use of refuges, a stepwise multiple regression was performed on the (arcsine-transformed) percentage of fish hiding at each observation. Due to the fact that no significant difference was found in the proportion of time spent in shelter between categories of fish (Table 2.1), this analysis was carried out on the overall percentages of both species combined that were observed in the refuges. It revealed that light intensity was the most important single explanatory variable and its effect was independent of that of date and temperature (see Table 2.2).

Table 2.2. Summary of the results from a stepwise multiple regression for the relative influence of light intensity, time of year (Julian date) and temperature on the use of refuges.

Variable	Order in which entered	t	P
Light	1	8.26	< 0.001
Temperature	2	9.62	< 0.001
Day	3	7.16	< 0.001

Overall: $r^2 = 0.333$, $F_{3,345} = 58.91$, $P < 0.001$

2.4.3 Effect of body size and treatment on the depth of water used

To compare the influence of absolute and relative body size on the position adopted by fish, a stepwise multiple regression was carried out on the mean zone in which a given fish was observed when out of shelter, irrespective of time of day or species. This illustrated that relative length was more important in predicting the position of fish than absolute length (Stepwise Multiple Regression: absolute length not included in model; model: $r^2 = 0.117$, $F_{1,142} = 19.94$, $P < 0.001$). Therefore relative length was used as the measure of body size in all subsequent analyses.

To test the first hypothesis that salmon prefer deep water, and my second hypothesis that they are displaced spatially by trout, I investigated the depth of water used by individual fish. For each fish, an indication of the depth of water used was calculated separately for day, twilight and night by averaging the zone use during each of these periods over the four days. The effect of treatment on distribution patterns was then analysed separately for daytime, twilight and night-time observations using analysis of covariance (ANCOVA), with fish category (allopatric salmon, sympatric salmon and sympatric trout) as the factor and relative body length as the covariate. There was a significant effect of relative body length on average position during the day (ANCOVA: effect of length: $F_{1,30} = 7.98$, $P = 0.008$), twilight ($F_{1,46} = 6.61$, $P = 0.013$) and night ($F_{1,56} = 9.18$, $P = 0.004$), with fish of greater length, relative to the other fish in their replicate group, being found in deeper water (see Fig. 2.3). The tendency for salmon to be mostly found in the deeper parts of the stream channels suggests that they, as well as trout, prefer deep water, thus supporting my first hypothesis. During the night there was also a significant effect of category of fish on average position (ANCOVA: comparison of regression slopes: $F_{2,54} = 0.37$, $P = 0.691$; comparison of regression elevations: $F_{2,56} = 4.07$, $P = 0.022$), with trout being found in deeper water than salmon of equivalent size in both allopatry and sympatry (see Fig. 2.3). There was, however, no significant difference in the depth of water used by salmon in allopatry and salmon in sympatry, thus providing no support for my second hypothesis.

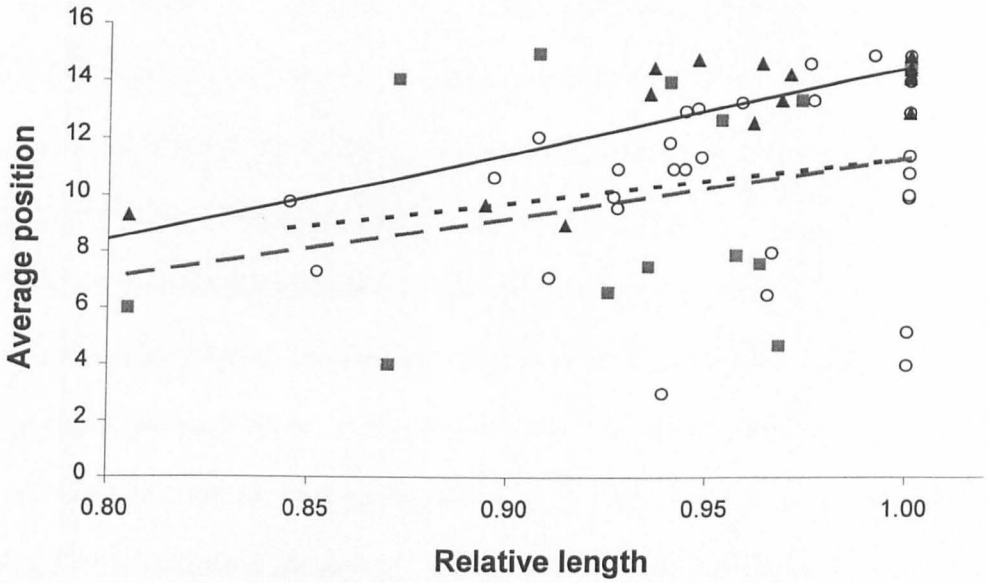

Figure 2.3. The average position of each fish whilst out of shelter during the night, plotted against relative length for salmon in allopatry (open circles; dotted line), salmon in sympatry (grey squares; grey dashed line) and trout in sympatry (solid triangles; solid line). Average position is calculated by averaging zone use during the night. Zone 15 is the deepest, thus slowest flowing water, whilst zone 1 is the shallowest and thus fastest flowing water. Similar trends were witnessed during daylight and twilight observations, however these are not presented for the sake of clarity.

2.4.4 Nocturnal versus diurnal activity

I used the calculated nocturnal index to test my third hypothesis that inter-specific competition results in a shift in diel activity and (or) temporal changes in habitat use by salmon. There was no significant difference between the nocturnal index (arcsine transformed) between salmon and trout when the two species were in sympatry (paired samples t-test: $t_7 = 1.50$, $P = 0.177$; see Fig. 2.4). However, there was a significant difference in the nocturnal index for salmon in allopatry and salmon in sympatry (independent samples t-test: $t_{14} = 2.39$, $P = 0.031$), with salmon in allopatry being more nocturnal (see Fig. 2.4). This supports my hypothesis that salmon undergo a shift in diel activity when they switch from allopatric to sympatric conditions. To determine the influence of body size on nocturnal versus diurnal activity for salmon in the two treatments, analysis of covariance was performed on the nocturnal index with treatment (allopatry and sympatry) as the factor and relative size as the covariate. This revealed a significant difference in the diel activity pattern of salmon of different lengths in the two treatments, with the largest salmon in a replicate group being the most nocturnal in allopatry but the least nocturnal in sympatry (ANCOVA: comparison of regression slopes: $F_{1,40} = 11.96$, $P = 0.001$; see Fig. 2.5).

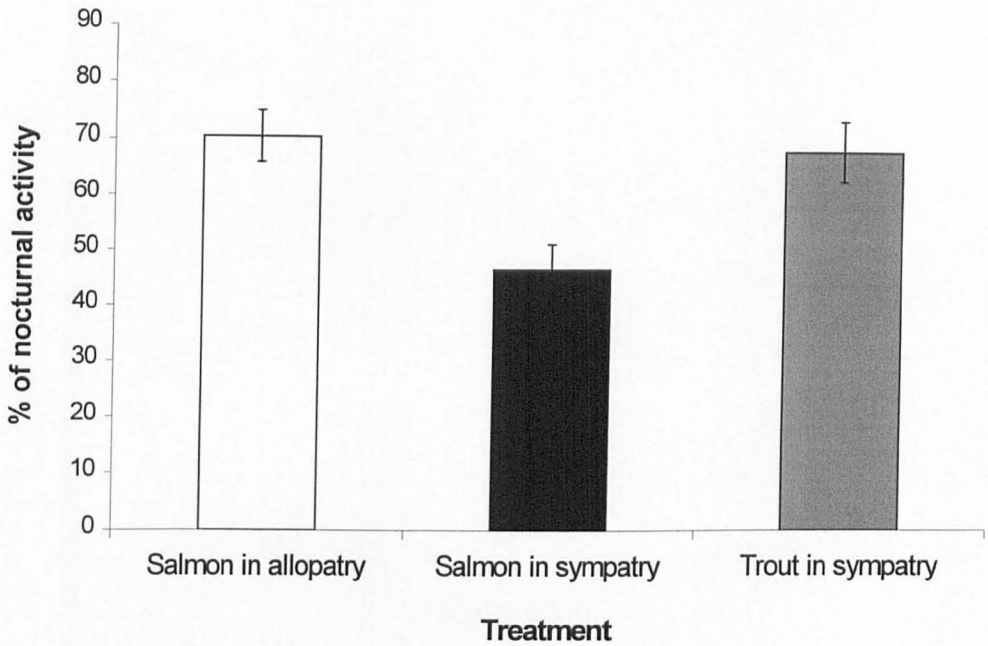

Figure 2.4. Percentage (±SEM) of nocturnal activity (where nocturnal activity = nocturnal activity/overall activity) for each treatment. Percentages are arcsine-transformed, therefore 90% nocturnal activity represents fish only active at night, whereas 0% nocturnal activity represents fish only active during the day.

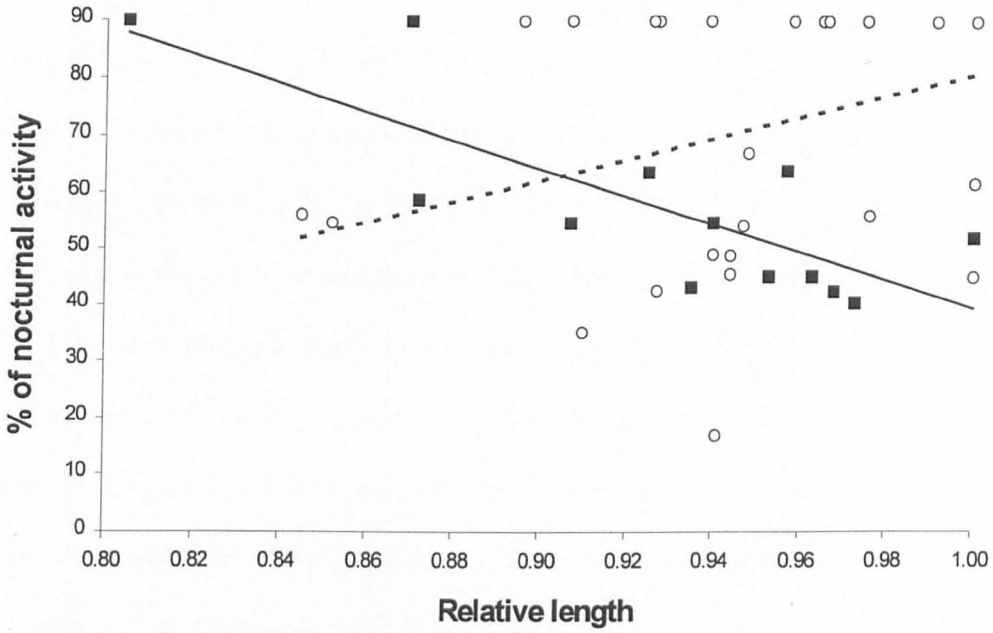

Figure 2.5. The percentage of nocturnal activity plotted against relative length for salmon in allopatry (open circles; dotted line) and salmon in sympatry (solid squares; solid line). Percentages are arcsine-transformed, therefore 90% nocturnal activity represents fish only active at night, whereas 0% nocturnal activity represents fish only active during the day.

2.4.5 Nearest-neighbour distances

In order to gain an insight into nearest-neighbour distances, the occasions when fish occurred in the same or adjacent zones were examined. Out of a total of 245 scan samples of the three test arenas at night, fish occurred in the same or adjacent zone on 83 occasions in allopatry and 125 occasions in sympatry. A chi-square goodness-of-fit test revealed that this represented a significant difference between the treatments ($\chi^2 = 8.48$, d.f. = 1, $p < 0.01$), with fish more likely to be in close proximity to each other in sympatry rather than allopatry. Interestingly, salmon in allopatry were in close proximity on 83 occasions, whereas in sympatry salmon only occurred in proximity with other salmon on two occasions, with trout being found in proximity with other trout on 55 occasions. A chi-square test revealed that this represented a significant difference between the two species ($\chi^2 = 49.28$, d.f. = 1, $p < 0.001$).

2.5 Discussion

2.5.1 Habitat preferences and activity patterns

My first hypothesis, that juvenile salmon in winter prefer deep water, was supported, with salmon preferring the deepest, and thus slowest-flowing water that was available. This preference was supported by the observation of the relatively larger fish holding deep-slow positions more frequently than relatively smaller fish, coupled with the fact that at this stage in the life-cycle of both

salmon and trout, dominant fish are larger than subordinates (Huntingford et al. 1990). Although this study does not differentiate between selection for water depth and water velocity, previous studies of both Atlantic salmon (Whalen & Parrish 1999) and brown trout (Cunjak & Power 1986; Mäki-Petäys et al. 1997) in the wild have shown a stronger selection for water velocity than water depth in winter. Therefore, the habitat preferences exhibited by Atlantic salmon could be considered to be a preference for slow-flowing water, occurring in areas of deep water, rather than a selection for deep water. A comparison of the average positions of brown trout in sympatry and Atlantic salmon in allopatry indicates that the trout had a stronger preference for deeper and (or) slow-flowing water, but their preferred microhabitat overlapped with that of the salmon. Rainbow trout (Riehle & Griffith 1993) and coho salmon (Nickelson et al. 1992) also prefer slow flowing water in winter. Similarly, coho salmon preferred deep pools offering protection from fast-flowing water and turbulence to deep pools that offered no shelter from high water velocities (Nickelson et al. 1992).

A comparison of the positions adopted by salmon in allopatry and in sympatry indicates that salmon were not significantly displaced from this preferred microhabitat by trout, thus providing no support for my second hypothesis. However, there is evidence of competition between the two species, with the data supporting my third hypothesis of a shift in the diel activity of Atlantic salmon caused by the presence of brown trout. The significant shift towards more daytime activity exhibited by salmon in sympatry, as opposed to salmon in allopatry, is evidence of the dominance of brown trout over Atlantic salmon. In

allopatry, the largest salmon were the most nocturnal and were found in the deepest water; that these are the dominant individuals suggests that this is the preferred spatial and temporal niche. Furthermore, their lack of daytime activity suggests that under allopatric conditions dominant salmon obtained enough food during the night to avoid risky daytime feeding. However, the presence of trout may have prevented these largest salmon from effectively feeding in deep water at night, causing them to become more active during the day. This is in accordance with earlier studies where salmon were shown to become more diurnal when food availability was reduced or nutritional requirements were increased (see Metcalfe et al. 1998, 1999). This result is also analogous to that found by Alanärä & Brännäs (1997), who observed individual rainbow trout and Arctic charr adopting contrasting diel activity patterns, apparently to reduce competition in accessing food. The similarity in the amount of time salmon and trout were observed to spend in refuges suggests that the two species have rather similar time budgets and feeding rates in relation to their nutritional needs.

2.5.2 Aggregations of fish and habitat partitioning

Previous studies of nocturnal activity during winter have witnessed no aggressive interactions between conspecifics of either Atlantic salmon (Whalen & Parrish 1999) or brown trout (Heggenes et al. 1993). Other studies have concluded that aggregations of trout in pools illustrates a cessation of territorial behaviour during the winter (Cunjak & Power 1986). However, the cessation of territorial behaviour in pools has also been witnessed at other times of year (Bremset &

Berg 1997), and may not be specially associated with winter. The lack of aggression noted in winter by Heggenes et al. (1993) was interpreted as an indication of a reduction in the need to feed, and hence to maintain territorial boundaries. Fraser et al. (1993) also noted that juvenile salmon were less aggressive at night and more tolerant of subordinates. However, this proximity may be due to the fact that an individual will defend a smaller area at night because the range at which prey can be detected decreases (Fraser & Metcalfe 1997), rather than to a total lack of territorial behaviour. Indeed in a tributary of Lake Superior characterised by low winter flow, salmon were aggressively maintaining positions at temperatures as low as 3 °C, with 53% of fish in dominance hierarchies (Healy & Lonzarich 2000). Despite the general consensus that there is a decrease in overt aggression between salmonids in winter, the results of this experiment indicate that competition for habitat and food does still occur.

The results suggest that aggregations and the general proximity of salmonids in winter, as reported by Cunjak & Power (1986) and Whalen & Parrish (1999), may not only result from a reduction in territorial aggression, but from the limited availability of preferred habitat. Limited availability of winter habitats may play a pivotal role in the number of salmonids that a stream can support (Nickelson et al. 1992; Cunjak 1996; Whalen & Parrish 1999).

The greater tendency for fish to have been found in close proximity when in sympatry than when in allopatry is likely to be a result of the difference in the use

of the water column by salmon and trout. Trout spent the majority of their time in the water column, whereas salmon were more likely to be on the substrate; this partitioning of the habitat may have allowed more fish to occupy the same area when there was a mixture of the two species. Bremset & Berg (1999) witnessed a similar segregation of salmon and trout, with trout holding position significantly further from the substrate than salmon. The tendency for trout to spend a higher proportion of their time in the water column may be a result of several factors, which are not mutually exclusive. Salmon have larger pectoral fins than trout and are thus better adapted for holding position on the substrate (Arnold et al. 1991). In addition, in artificial stream environments where most food is distributed in the water column rather than in the benthos, salmon always appear to move upwards to take food items at night. This is probably because the silhouette of a food item against the sky allows salmon to see and capture food items more easily. Thus salmon will sit on the bottom at night so that they can get underneath all potential prey items (Valdimarsson & Metcalfe 1999). The positioning of trout above salmon in the water column when in sympatry will therefore deplete the food supply available to salmon. Thus, the shift to more diurnal activity by salmon may not be caused by overt aggression by trout, but by trout monopolising the available food in the water column. Salmon and trout may both spend less time on the substrate during the day in order to take advantage of surface drift, which is not visible to them during the night.

2.5.3 Implications

Recent experimental studies have shown that the trade-off between diurnal and nocturnal foraging is complex and may be related to a number of factors such as food availability, feeding efficiency, life-history strategy, water velocity and predation risk (Metcalfe et al. 1997, 1998, 1999). The results of this study suggest that inter-specific competition can also affect the trade-off between nocturnal and diurnal foraging.

There are also widespread management implications arising from this study. First, the results reinforce previous reports of the importance of slow-flowing water to juvenile salmonids in winter. That this habitat requirement is often limited (Rimmer et al. 1985; Cunjak & Power 1986; Cunjak 1996) may have profound effects on those species known to depend upon it. The susceptibility of these species to habitat limitations may be further increased by the fact that, although during summer different age-groups of fish select different habitats (Kennedy & Strange 1982), in winter young-of-the-year and post-young-of-the-year Atlantic salmon have been found to use similar microhabitats (Whalen & Parrish 1999). Secondly, the results indicate that competition between Atlantic salmon and brown trout for resources such as habitat and food is not restricted to the summer months, during which time it has previously been shown to occur (Kennedy & Strange 1986a,b). The most immediate effect of this competition is that salmon mortality due to predation may increase during the winter if they are forced to become more active during the day (Metcalfe et al. 1999). Longer-term

survival rates of salmon may also be affected by inter-specific competition with trout. Salmon destined to smolt and migrate to sea in the spring continue to grow during the winter months (Metcalfe et al. 1988). Since the survival of migrating individuals is size dependent (Lundqvist et al. 1994), reduced over-winter growth of salmon due to competition with trout may lead to decreased chance of survival.

The potential of a stream to produce high numbers of good quality salmon smolts does not only depend on the availability of winter habitat, as suggested by Nickelson et al. (1992), but also on the presence of brown trout, which may affect the growth and survival of over-wintering salmon. The importance of winter habitat to smolt production has recently been confirmed through a winter habitat modification study in which the overwinter survival and smolt production of coho salmon increased in treatment streams in comparison to unmodified, control streams (Solazzi et al. 2000). Similar comparative studies are needed to determine the effects of brown trout on the overwinter survival and size of Atlantic salmon smolts.

CHAPTER 3: INTRA- AND INTER-SPECIFIC COMPETITION FOR WINTER CONCEALMENT HABITAT IN JUVENILE SALMONIDS

3.1 Abstract

The availability of stream-bed refuges has previously been shown to be of critical importance to the survival of over-wintering juvenile salmonids. I used semi-natural stream channels to quantify intra- and inter-specific competition for daytime refuges and the willingness of Atlantic salmon and brown trout to share available shelter. Refuge use was frequently associated with aggressive behaviour when two fish were provided with only one shelter, with intra- and inter-specific competition being similar in intensity. Resident individuals were less likely to leave the refuge than were intruders and sharing of refuges was uncommon, both when competing for one shelter (experiment I) and when these were provided in excess (experiment II). Fish showed greater preferences for foraging habitat during the night than for the location of daytime shelters, and were therefore willing to shift habitats in order to find adequate shelter. Overall, these results suggest that winter competition for refuges, both within and between species of salmonid, is likely to be intense if refuge availability is limited in the wild.

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3.2 Introduction

Sheltering behaviour is widespread among both invertebrates and vertebrates and can be used to investigate the trade-off between the cost of lost feeding opportunities and the benefit of predator avoidance during an individual's decision-making processes (Dill & Fraser 1997; Sih 1997; Krause et al. 1998). For example, Dill & Fraser (1997) were able to measure a cost of sheltering in terms of lost growth in a sedentary polychaete worm which filter feeds at the mouth of its calcareous tube but retreats when threatened. Shelter use can influence an individual's chance of survival, particularly through a decreased risk of inter- and intra-specific predation. Predator avoidance has been cited as the primary function of sheltering behaviour in salmonid fishes (Gregory & Griffith 1996a; Valdimarsson & Metcalfe 1998). However, in nature the ability to find a suitable refuge can also have other benefits. For example, Smith & Griffith (1994) found that rainbow trout survival in winter was higher in enclosures with cobble substrate than in those without, even though both enclosures excluded predators. The presence of rocks in the enclosures allowed trout to shelter in interstitial spaces that provided them not only with protection against physical damage from dislodged ice moving in the water column, but also a reduction in daytime energy expenditure and a thermal benefit since temperatures in the interstitial spaces were higher than in the water column. The ability to find adequate shelter can therefore influence survival under natural conditions, independent of predation.

Winter can be a bottleneck during which density-dependent processes occur in some populations of salmonid fish (Bjornn 1971; Mason 1976), with availability of suitable habitat being cited as one of the main limiting factors (Rimmer et al. 1985; Nickelson et al. 1992; Cunjak 1996). There are two types of preferred winter habitat important to the survival of fishes. First, slow-flowing water has been shown to be important for over-wintering salmonids (e.g. Heggenes et al. 1993; Whalen & Parrish 1999; chapter 2). Secondly, cobble-boulder substrates that provide shelter have been found to be of critical importance for both stream-dwelling salmonids and cyprinids (see Cunjak 1996). Habitat enhancement programmes have highlighted the importance of both habitats. Solazzi et al. (2000) have shown that the addition of large woody debris to newly created dammed pools provides salmonids with refuge from high-velocity conditions and improves over-wintering survival of coho salmon, cutthroat trout and rainbow trout, as well as increasing coho salmon smolt production. Similarly, the addition of patches of cobble to a stream in Idaho increased the number of over-wintering chinook salmon eightfold over numbers from the previous winter, despite numbers being comparable at the onset of the two winters (Hillman et al. 1987).

The importance of shelters in salmonid ecology is not restricted to the winter months, with some species of salmonid also sheltering during the day in summer (Rimmer et al. 1984; Gries et al. 1997; Gries & Juanes 1998). Despite the significance of shelters, few studies have examined whether fish actively compete for or defend refuges. This is largely because fish are thought to become less aggressive during winter (McMahon & Hartman 1989; Fraser et al.

1993), whilst studies in summer have concentrated on territorial disputes over food rather than shelter resources (e.g. Fausch 1984). McMahon & Hartman (1989) and Glova (1986) both reported territorial behaviour amongst cover in juvenile coho salmon and cutthroat trout respectively, however, only Gregory & Griffith (1996b) have quantified the aggression associated with shelter use.

Here I report more detailed investigations into competition for refuges than have previously been conducted. In my first experiment, where shelter availability was limited, I provide the first quantitative assessment of shelter competition among conspecific and heterospecific pairs of Atlantic salmon and brown trout. I test for asymmetry in the abilities of Atlantic salmon and brown trout to compete for shelter during winter. Aggressive behaviour and shelter sharing were observed at dawn, when movement into shelters is at its peak (Gregory & Griffith 1996b). In experiment II, when shelters were provided in excess, I examined the frequency of shelter sharing among allopatric groups of salmon, and sympatric groups of Atlantic salmon and brown trout. The influence of surrounding habitat type on refuge use was also investigated.

3.3 Methods

3.3.1 Experiment I

This experiment was carried out in a glass stream-channel system at the University of Glasgow, U.K. The channel consisted of a stack of three glass tanks measuring 180 x 25 x 20 cm and one glass tank measuring 120 x 25 x 20

cm, which were interconnected by plastic pipes. These tanks then drained into two 60-litre sumps from which water was recirculated by pumping it to the top stream tank. The stream channel system was positioned within a temperature-controlled laboratory. In order that the lighting regime could be controlled separately for each glass tank, the system was surrounded by black polythene sheeting to cut out any light from the laboratory. An observation hide was also created so that fish could be observed without casting any external light on the tanks. The glass tanks had a 4 cm layer of gravel substrate, a water depth of 11 cm and a flow rate of approximately 0.03 $m \cdot s^{-1}$. Partitions placed within the tanks created compartments; the partitions were opaque but had panels of fine mesh to allow a directional current through the tanks. The compartments in which the experiments were conducted, hereafter referred to as experimental arenas, measured 40 x 25 cm. Six experimental arenas were used in total, two in each of the longer glass tanks. A feeder and a shelter were placed in opposite corners of each arena so that fish could not feed whilst in the shelter. The feeders were 25 ml universal tubes with a small hole drilled near the top to allow water to circulate, and a small hole (1.5 mm in diameter) near the bottom to allow a mixture of live *Daphnia* and chironomid larvae to escape at random times after having been placed in the feeder. A plastic mount held each universal tube so that the exit hole for the larvae was 5.5 cm above the substrate. The shelters were made from 1-L opaque plastic bottles cut lengthwise into quarters and embedded in the gravel, creating cavities in the gravel measuring 15 x 4 x 4 cm. Fish could enter the shelters through a 4 x 4 cm hole cut into the top of each shelter. These shelters were placed at the downstream end of each section with

the open side against the glass wall of the tank, allowing any fish within them to be identified (see Valdimarsson et al. 1997).

The fish used were wild-caught Atlantic salmon (fork length: mean ± SE = 65.5 ± 1.07 mm; weight = 2.64 ± 0.13 g) and brown trout (fork length = 76.7 ± 1.62 mm; weight = 4.28 ± 0.28 g) from the River Endrick which flows into Loch Lomond, west Scotland. These fish were used in one of three treatments. Allopatric trials (either two salmon or two trout) were used to examine intra-specific competition for shelters in each species, whilst sympatric trials (one salmon and one trout) were used to study inter-specific competition for shelters. Fish in all three treatments were size-matched to reduce any confounding effects of large size differences. Fish were individually marked on their caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Fish were then placed in experimental arenas on the evening before observations began and light intensity was reduced to night-time levels (0.01 lx) thirty minutes after fish had been placed in the arena. Light intensity was recorded using a photometer (Skye Instruments SKL 300, range 0.01-2000 lx) placed alongside the experimental arena.

Light intensity was controlled by the use of three dimmer switches, each of which controlled two bulbs that were situated above the two experimental arenas located on each shelf. To simulate natural dawn conditions, light levels were gradually increased by 33 lx every five minutes for 45 minutes, reaching a maximum of approximately 300 lx. The position of each fish (either in or out of shelter) was recorded immediately before the dawn light manipulation and then

every five minutes over the 45-minute dawn observation period. During this same period, continuous observations of feeding attempts, aggressive behaviour and movement in and out of the shelter were made. For each aggressive interaction the location and identity of aggressor and recipient was noted. Any movement by the recipient between habitats was also noted (fish were defined as being forced to move habitats if they moved in or out of shelter within five seconds of having been attacked). Since only two arenas could be monitored simultaneously, the timing of the simulated dawn was staggered so that data could be obtained from all six arenas each day. After the dawn period, light levels were kept constant at approximately 300 lx for eight hours in each tank, after which light levels were reduced directly to 0.01 lx until 'dawn' the next morning. The fish were fed 1% of their body weight per day, with the feeders being replenished with *Daphnia* and chironomids immediately before light levels were reduced in the evening, and immediately after all observations had been carried out in the morning. Equal amounts of food were given in the morning and in the evening.

Observations were made on four successive mornings, after which time the fish were removed and replaced by new groups. All three treatments were replicated eight times, with all fish being used only once. Water temperature was continuously measured using a digital thermometer placed in the stream tank and varied between 6.9 and 10.3 °C during the course of the experiment, which ran between 7th February and 8th March 2001.

3.3.2 Experiment II

A full description of the materials and methods for this experiment is given in chapter 2, and only details relevant to shelter use are presented here. The experiment consisted of monitoring habitat and shelter use by salmon and trout in a semi-natural outdoor stream channel at the University Field Station, Rowardennan, Scotland. In a series of replicated trials, groups of four salmon (allopatric treatment) and two salmon with two trout (sympatric treatment) were observed in identical experimental arenas, each of which had a gradual increase in water depth from 10 cm at the upstream end to 45 cm at the downstream end. Accordingly, the surface velocity of the water varied continuously from 0.16 m · s^{-1} at the upstream end to 0.03 m · s^{-1} at the downstream end. Each experimental arena was 225 x 60 cm and the outer side of the channel was marked every 15 cm, to define 15 zones per arena (with zone 1 being at the upstream end) and allow referencing of the recorded positions of each fish. The arenas were landscaped with fine gravel (5-25 mm diameter) to prevent fish from hiding in stream-bed cavities. Six shelters were placed at regular intervals in each of the experimental arenas with the open side against the glass wall to allow any fish within them to be identified by their alcian blue marks (see below). The shelters were made from 1-L opaque bottles that were cut lengthwise in half, creating cavities in the gravel measuring 17 x 8.5 x 4.25 cm. Hence in this experiment, stream-bed shelters were provided in excess.

Water was pumped constantly from Loch Lomond into the stream channel and ranged in temperature from 4.3 to 6.1 °C. Light conditions and photoperiod for

the outdoor stream channel were the same as the ambient conditions of Loch Lomond. Fish were provided with 0.5% of their total body weight in food per day. The food was delivered via a belt feeder that dropped pelleted food at a trickle rate at the upstream end of each arena. The fish used were wild-caught Atlantic salmon (fork length: mean ± SE = 109.4 ± 1.83 mm; weight = 13.42 ± 0.65 g) and brown trout (fork length = 100.7 ± 2.77 mm; weight = 9.87 ± 0.90 g) from the River Blane, a tributary of the River Endrick. Fish were size-matched in each treatment to reduce any confounding effects of large size differences, and individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Fish were then allowed to reside in the experimental arenas for a period of 72 h before observations began.

Observations on each group of acclimated fish were made on four consecutive dates. Each observation period lasted seven hours and covered the day-night transition at either dusk or dawn. During each observation period the position of each fish was recorded every 30 minutes by scanning briefly with a flashlight, a method chosen to minimise the disturbance of the fish (see Heggenes et al. 1993). Data collected during each scan observation included the zone number in which each fish was located (1-15), or the shelter in which the fish was hiding (1-6, with shelter 1 being at the upstream end). Light intensity and water temperature were also noted. Light intensity was measured using a Skye Instruments SKL 300 photometer (range 0.01 – 2000 lx) and recorded as the mean of two measurements made just above the water surface. Water temperature was measured using a digital thermometer placed permanently in the

stream. After the data for each group were collected, the fish were removed and different fish were placed in the test arena. Both treatments were replicated eight times; all fish were used only once. The experiments were carried out between 16th January and 4th March 1999.

3.3.3 Data analysis and statistical treatment

3.3.3.1 Experiment I

To determine whether fish increased their use of shelter as the simulated dawn period progressed, I calculated the mean percentage of observations in which each individual fish was in shelter over the four days at the start point (dimmest), and end point (brightest) of each observation period. The mean for each replicate was then calculated and used in a paired samples t-test. To examine the occurrence of shelter sharing in the different treatments I calculated the percentage of all observations in which both fish were found occupying the shelter. I used one-way analysis of variance (ANOVA) to determine whether there were any species or treatment effects on the percentage of time that fish spent sharing shelters, using replicate mean values as data points. Analysis of covariance (ANCOVA) was used to determine whether absolute size (averaged for the two fish within a replicate), or the size difference between the two fish in a replicate, had any effect on the amount of time that fish spent sharing shelters. The analyses described above were used to investigate overall trends in shelter use, and therefore when calculating the replicate means in the sympatric treatment the two species were not treated separately. However, when calculating replicate means for all subsequent analyses, salmon and trout in

sympatry were treated separately in order that the behaviour of each species under allopatric and sympatric conditions could be compared. Fish were therefore divided into the following categories: salmon in allopatry, trout in allopatry, salmon in sympatry (with trout), and trout in sympatry (with salmon). Two-way ANOVA was used to determine which species (trout or salmon) spent most time in shelter under allopatric conditions, and ascertain whether the larger fish of a pair was able to monopolise shelter. The percentage of observations in shelter over the whole trial was the dependent variable and size (larger or smaller of a pair) and species (salmon or trout) were the fixed factors. Paired samples t-tests were used to test for similar relationships in the sympatric trials.

Data on aggression were analysed by calculating the rate of aggression per minute for each individual and then calculating replicate means, whilst maintaining the integrity of species data in the sympatric trials. The rate of aggression both in and out of the shelter was also calculated, controlling for the time fish spent in different habitats by using only observation periods in which both fish started in the same habitat (either in or out of shelter). Separate two-way ANOVAs were used to determine whether there was any difference between allopatry and sympatry in the percentage of aggressive interactions that forced a habitat switch in salmon and trout. The percentage of aggressive interactions that forced a habitat switch was the dependent factor with category of fish (allopatry or sympatry) and the direction of enforced change (into or out of shelter) as the fixed factors. To determine whether there was a prior residence effect on shelter use, the number of occasions when a fish entered an already occupied shelter was counted along with the percentage of such times when the

intruder left before the resident, and vice versa. The relationship between the percentage of times the intruder left before the resident, and the relative length of the intruder (its body length as a percentage of that of the resident) was investigated using linear regression. Finally, as a result of the temperature fluctuations that occurred over the course of the experiment, regressions were carried out to determine whether temperature had an effect on the rate of aggression or the percentage of time fish spent sharing shelters.

3.3.3.2 Experiment II

A comparison of the overall percentage of time that fish spent sharing in allopatry and sympatry was undertaken in an identical manner to that for Experiment I, by calculating overall replicate means. The percentage of time spent sharing with the same or different species during the sympatric trials was calculated by taking a mean for the two salmon in a replicate, and a mean for the two trout, thus preserving the integrity of the species data. When determining whether fish preferred to share with the same or different species in sympatry it was necessary to control for the number of fish of each species type. Because there were four fish in each replicate trial, each fish had a one in three chance of sharing with a conspecific sheltermate and a two in three chance of sheltering with a heterospecific sheltermate. Therefore, the percentage of time spent sharing with conspecifics was multiplied by one-third, whilst the percentage of time spent sharing with the heterospecifics was multiplied by two-thirds. These values were then compared using a Mann-Whitney U-test. A Wilcoxon's signed

rank test was used to determine whether salmon shared with other salmon more frequently than trout shared with other trout.

For the purpose of comparing the relative use of different habitats for foraging and for sheltering, zones were divided into those in deep water (zones 11-15), shallow water (zones 1-5) and water of intermediate depth (zones 6-10). The six shelters were categorised in a similar manner with shelters in deep (5 and 6), intermediate (3 and 4) and shallow (1 and 2) water. Analysis of covariance was then used to examine the relationship between the percentage of time in deep shelters (dependent factor) and the percentage of foraging (i.e. non-sheltering) time in deep zones (covariate), with category of fish (salmon in allopatry; salmon in sympatry; trout in sympatry) as the fixed factor. To determine the relative importance of using shelters located in deep water and the use of deep water for foraging I used a Wilcoxon's signed rank test to compare the percentage of observations of sheltering in which an individual was in deep shelters with the percentage of foraging observations in which an individual was recorded in deep zones.

For both experiments all percentage data were normalised by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for two-tailed tests of significance.

3.4 Results

3.4.1 Experiment I

There was a significant increase in the use of shelters from the start to the end of the simulated dawn period when considering all replicates of the three treatments (paired samples t-test: $t_{23} = 2.56$, $P = 0.018$; Fig. 3.1), indicating that the increase in light intensity at dawn prompted fish to seek shelter. There were no significant differences between species or treatments in the percentage of time over the dawn observation period that fish spent sharing shelters (one-way ANOVA: $F_{2,23} = 1.06$, $P = 0.364$; salmon in allopatry: 21.7 ± 5.27 % (mean ± S.E. mean); trout in allopatry: 18.9 ± 6.39 %; sympatry: 10.4 ± 5.30 %). There was a significant trend for larger salmon in allopatry and trout in allopatry to share more often than smaller salmon and trout. However, when the two species occurred together in sympatry, larger fish shared less often than smaller fish (ANCOVA: comparison of regression slopes: $F_{2,18} = 4.86$, $P = 0.020$). There was, however, a lot of noise in the regression equations with the relationship for trout in allopatry in particular being driven by one outlier. There was no significant relationship between the percentage of time the shelter was shared and the weight difference between the two fish in a replicate (ANCOVA, comparison of regression slopes: $F_{2,18} = 2.97$, $P = 0.077$; effect of weight difference: $F_{1,20} = 0.14$, $P = 0.715$; comparison of regression elevations (effect of treatment): $F_{2,20} = 1.01$, $P = 0.384$).

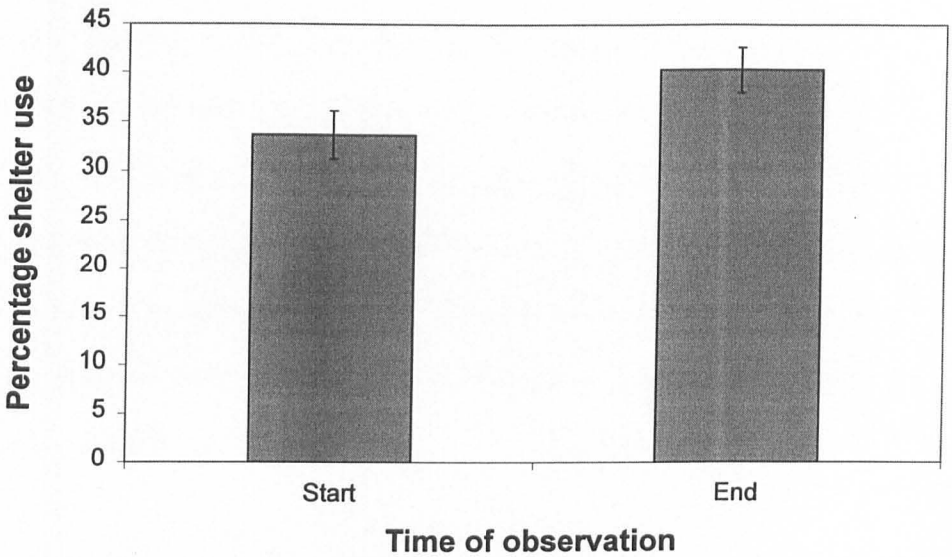
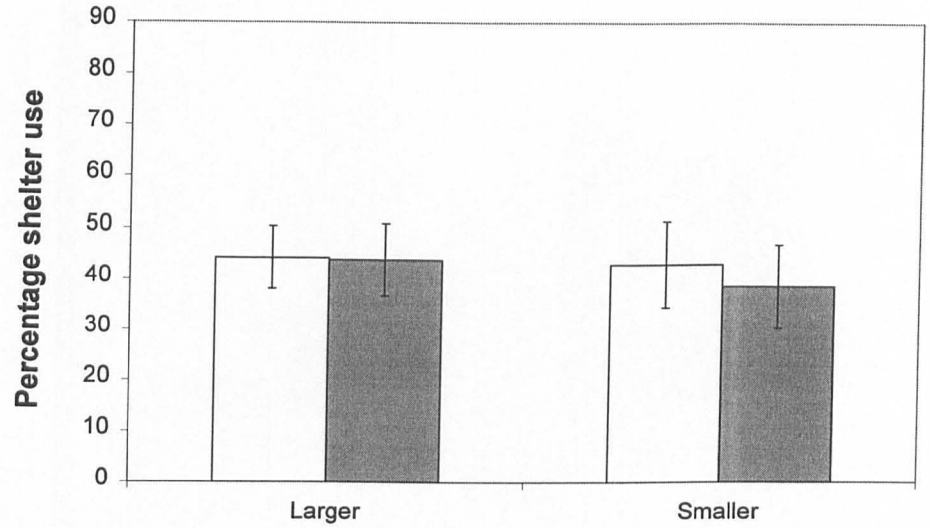


Figure 3.1. Percentage of observations (±SEM) spent in shelters for individuals from all treatments at the start and end of daily dawn observation periods in Experiment I. Percentages are arcsine-transformed, thus a value of 45 corresponds to equal amounts of time spent in and out of shelter.

There was no significant difference between categories of fish in the rate at which fish were observed to enter the shelter (one-way ANOVA: $F_{3,31} = 0.37$, P = 0.773). There was no effect of an individual's body size (two-way ANOVA, effect of size: $F_{1,29} = 0.20$, P = 0.657) or species (effect of species: $F_{1,29} = 0.11$, P = 0.747) on the percentage of observations that fish in allopatry were found in shelter (Fig. 3.2a). However, in sympatry, there was a significant effect of relative body size (paired samples t-test: $t_7 = 4.47$, P = 0.003), with the larger fish in a pair spending more time in the shelter over the dawn period than the smaller fish, although there was no difference between the two species (paired samples t-test: $t_7 = 0.68$, P = 0.518; Fig. 3.2b).

There was no significant difference in the rate of aggression by salmon and trout, either in allopatry or sympatry (one-way ANOVA: $F_{3,31} = 1.84$, P = 0.163). There was also no significant difference in the amount of aggression that was initiated in, as opposed to out of shelter (non parametric two-way ANOVA, Sheirer-Ray-Hare test (Dytham 1999): effect of being in or out of shelter: $\chi^2 = 0.93$, d.f. = 1, P = 0.761; effect of category of fish: $\chi^2 = 1.58$, d.f. = 3, P = 0.663; interaction between category and position: $\chi^2 = 0.41$, d.f. = 1, P = 0.998). For both salmon in allopatry and salmon in sympatry, a higher percentage of aggressive interactions forced fish out of shelters than forced fish into shelter (two-way ANOVA, effect of category of fish: $F_{1,17} = 0.12$, P = 0.731; effect of context of aggression: $F_{1,17} = 12.53$, P = 0.003; Fig. 3.3a). A similar result was found for trout in both allopatry and sympatry (two-way ANOVA, effect of category of fish: $F_{1,20} = 0.18$, P = 0.679; effect of context of aggression: $F_{1,20} = 7.43$, P = 0.013; Fig. 3.3b).

a)



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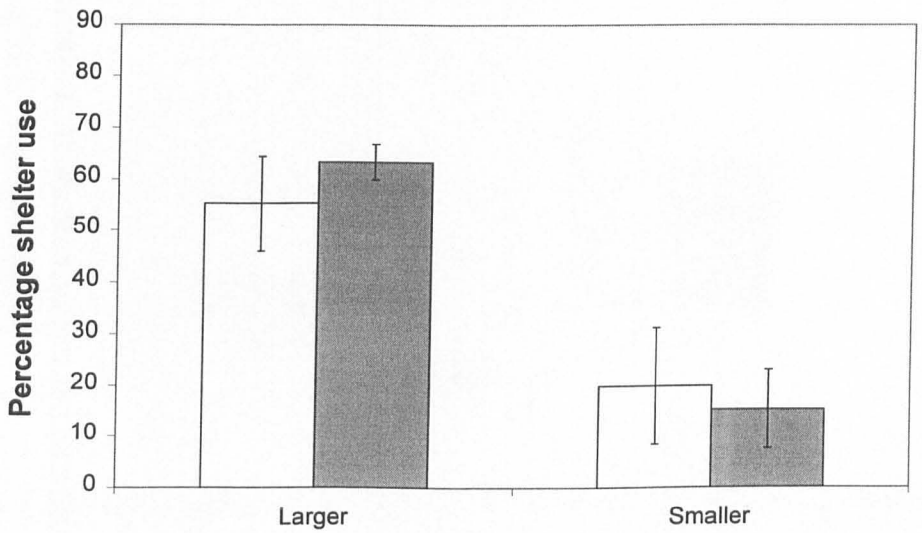
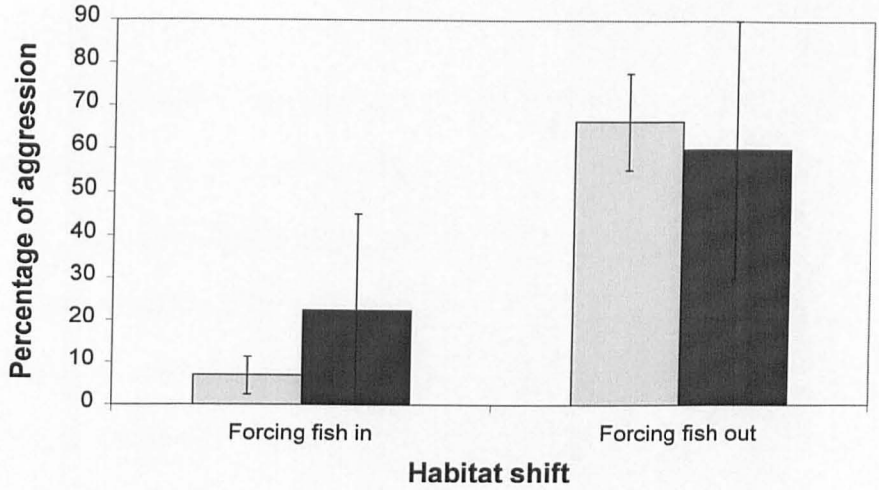


Figure 3.2. Shelter use in Experiment I in relation to relative body size. Percentage of time (±SEM) spent in shelters for the larger and smaller fish in a pair for a) allopatric salmon (open bars) and trout (shaded bars); and b) sympatric salmon (open bars) and trout (shaded bars). Percentages are arcsine-transformed.

a)



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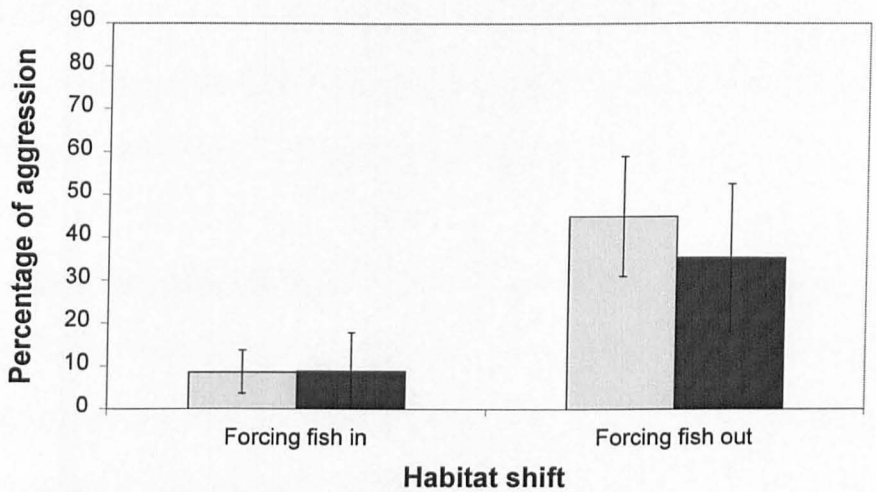

Figure 3.3. Consequences of aggression in Experiment I. Percentage (±SEM) of the aggressive interactions occurring when both fish were outside of the shelter that led to one fish being forced into shelter, and percentage of aggressive interactions that occurred when both fish were inside the shelter that forced one fish out for a) allopatric (shaded bars) and sympatric salmon (filled bars); and b) allopatric (shaded bars) and sympatric trout (filled bars). Percentages are arcsine-transformed, thus a value of 90% represents a situation where aggression always forced the other fish to shift habitats.

The first fish to enter the shelter during an observation period was recorded on 80 occasions, and in 55 of these cases this first fish was the larger of the pair, a significantly higher proportion than would be expected by chance (χ^2 = 10.51, d.f. = 1, P < 0.01). There was no significant difference between treatments in the percentage of times the larger fish entered first (one-way ANOVA: $F_{2,21}$ = 2.11, P = 0.146), although there was a trend for the larger fish in sympatry to enter first on more occasions (75.7 ± 7.5 %, mean ± S.E.) than the larger fish in allopatry (salmon in allopatry: 43.8 ± 14.8 %; trout in allopatry: 53.7 ± 10.2 %). On entering an already occupied shelter, the intruder left first significantly more times than did the resident (percentage of occasions that intruder left first: salmon in allopatry: 76.6%; trout in allopatry: 75.0%; sympatry: 77.8%; χ^2 = 21.78, d.f. = 1, P < 0.001). Size was also a factor in predicting which fish left first, with larger intruders less likely to leave before the resident than smaller intruders (regression: r^2 = 0.23, $F_{1,24}$ = 7.34, P = 0.012; Fig. 3.4).

Temperature had no significant effect on either the rate of aggression (regression: r^2 = 0.019, $F_{1,94}$ = 1.79, P = 0.185) or on the percentage of fish sharing shelters (regression: r^2 = 0.002, $F_{1,94}$ = 0.16, P = 0.694), possibly because of the narrow temperature range during the experimental period.

3.4.2 Experiment II

There was no significant difference between the allopatric and sympatric treatments in the percentage of time that fish spent sharing (Mann-Whitney U-test: U = 21.0, z = -1.16, P = 0.244). In sympatry, neither salmon nor trout

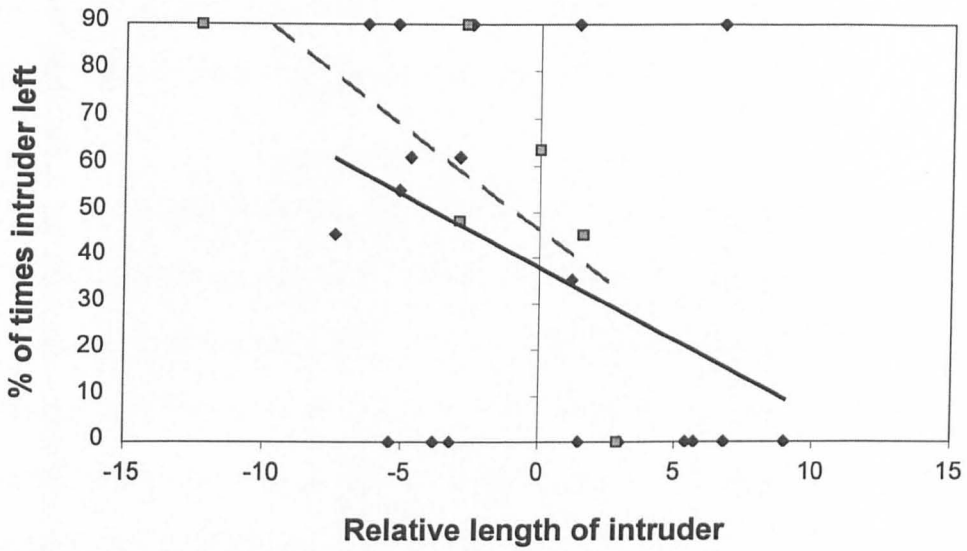

Figure 3.4. Percentage of times in Experiment I that, on entering an already occupied shelter, the intruding fish then left before the prior resident. Percentages plotted with respect to the relative length (expressed as percentage size difference from the resident), for fish in allopatry (filled diamonds; solid regression line – see text for analysis) and fish in sympatry (shaded squares, dashed line). Percentages are arcsine-transformed, thus intruders with a value of 90% always left the shelter before the resident.

showed a preference for sharing with conspecific over heterospecific sheltermates (Mann-Whitney U-test: $U = 29.0$, $z = -0.38$, $P = 0.702$). There was also no significant difference in the sympatric treatment between the amount of time salmon spent sharing with salmon and the amount of time trout spent sharing with trout (Wilcoxon's signed rank test: $z = -0.447$, $P = 0.655$).

There was a significant positive relationship between the percentage of observations where an individual fish was recorded in deep zones when out of refuges (presumed foraging) and the percentage of observations where fish were occupying shelters in deep water, for all categories of fish (ANCOVA, comparison of regression slopes: $F_{2,49} = 0.88$, $P = 0.423$; effect of zone use: $F_{1,51} = 7.46$, $P = 0.009$; comparison of regression elevations: $F_{2,51} = 0.30$, $P = 0.743$; Fig. 3.5). However, the preference for deep zones when out of shelters was stronger than the preference for deep shelters. Thus the percentage of foraging observations in which an individual was recorded in deep zones was generally greater than the percentage of observations of sheltering in which it was recorded in deep-water shelters (Wilcoxon's signed rank test: $z = -4.461$, $P < 0.001$).

3.5 Discussion

My experiments show that Atlantic salmon and brown trout compete for daytime shelters during winter, and that intra- and inter-specific competition can be equal in intensity. Experiment I shows that there was a prior residence effect involved in the resolution of contests over shelters, while experiment II suggests that fish were willing to shift habitats in order to find adequate shelter. These findings

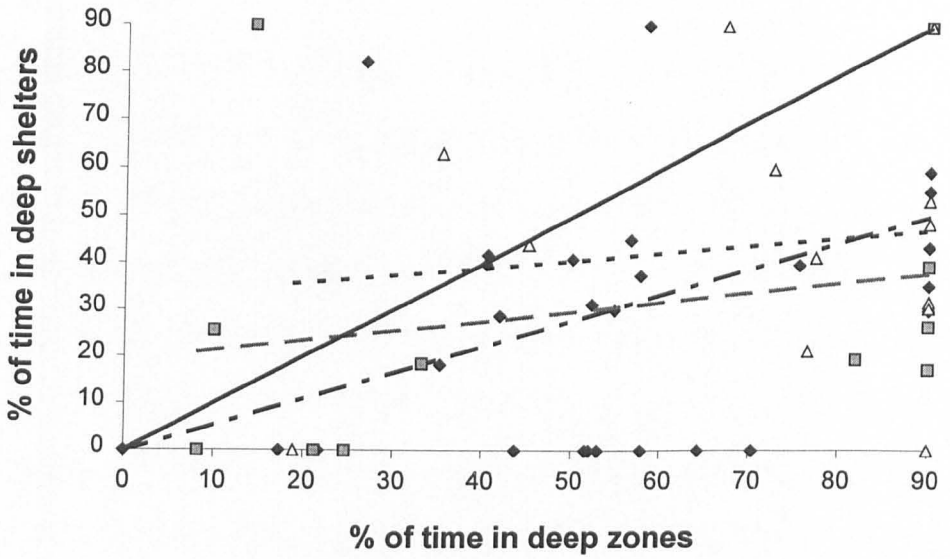

Figure 3.5. Percentage of observations of sheltering in Experiment II in which the fish was in deep shelters against percentage of observations of the same fish out of shelter in which it was in deep zones. Data plotted separately for salmon in allopatry (filled diamonds; dotted-dashed line), salmon in sympatry (shaded squares; dashed line) and trout in sympatry (open triangles; dotted line). Solid black line represents equal percentage of observations in deep shelters and deep zones; percentages are arcsine-transformed.

and the implications of this competition are discussed below with reference to other relevant work.

Fish of both species increased their use of shelters during dawn as light intensity increased in experiment I, as predicted based on previous work in which salmonids have been found to be active at night but then seek shelter during daylight in winter (e.g. Heggenes et al. 1993; Fraser et al. 1993). The frequency with which fish shared shelters was low in both of my experiments, supporting previous studies on salmonid sheltering behaviour in which the use of refuges was almost exclusively by single fish both in winter (Glova 1986; Cunjak 1988; Gregory & Griffith 1996a) and summer (Rimmer et al. 1983; Gries & Juanes 1998). Armstrong & Griffiths (2001), using wild fish in a semi-natural stream channel, found that shelter use was density dependent with the mean number of fish per refuge being ≤ 1.5 even at densities that would result in 5 fish per shelter if all fish were sheltering simultaneously. Most previous work therefore shows that salmonids do not share shelters with conspecifics, suggesting intra-specific competition for shelters would arise if refuges were limited in number.

There was no difference in either of my experiments in the frequency with which fish shared shelter with members of the same and different species, suggesting that shelters were of equal importance to both species and that intra- and inter-specific competition for shelters was equivalent in intensity. This is supported by the fact that salmon and trout initiated similar levels of aggression in experiment I, both in allopatry and sympatry. This result is surprising as trout are normally considered to be more aggressive than salmon of a similar size

(Kalleberg 1958; Kennedy & Strange 1986b), and may reflect the importance of shelter to both species. The rate of aggression witnessed in this study (overall mean of 0.030 interactions per fish per minute in experiment I) was similar to the rate observed between rainbow trout competing for shelters in a laboratory stream (Gregory & Griffith 1996b). Although these rates of aggression are lower than those reported for salmonid populations in summer (e.g. Hartman 1965) and the onset of winter is associated with a reduction in aggressive behaviour associated with feeding territories (Heggenes et al. 1993; Fraser et al. 1993), individuals still compete for shelters. Chapter 2 shows that intra- and inter-specific competition for deep, slow-flowing water also occurs in winter indicating that competition for limited resources occurs throughout the year, not simply during the summer when individuals compete for food (e.g. Fausch 1984).

Aggression inside shelters during experiment I was commonly followed by one fish then moving outside, whereas aggression out of shelters did not usually lead to either fish entering a shelter. This suggests that aggressive attacks within a shelter served to drive a competitor out. Gregory & Griffith (1996b) also provide indirect evidence that the majority of aggression that they observed was related to competition for shelters, because significantly more aggressive acts occurred during the initial concealment period (first 90 minutes of daylight) than during the rest of the day.

Competition for shelters among underyearling rainbow trout was related to the size of individuals, with one of the larger fish within a group defending a shelter

and initiating almost 80% of the aggression (Gregory & Griffith 1996b). In experiment I, individual Atlantic salmon and brown trout did not monopolise shelters or perform aggressive acts in such a manner under allopatric conditions. However, when in sympatry the largest individual tended to gain a disproportionate share of the shelter, irrespective of its species identity. These contrasting results may be explained by the prior residence effect which dictates that a holder of a territory or shelter has an advantage over intruders and is more likely to win contests for that resource (e.g. Tobias 1997; Figler et al. 1999; chapter 4). Evidence for a prior residence effect on shelter use was witnessed in all three treatments, with the intruder to an occupied shelter leaving first significantly more often than the resident did. This prior residence effect was related to body size, with relatively larger intruders less likely to leave before the resident than were smaller intruders. Although there was no significant difference in the mean percentage of times that the larger fish of a pair entered first in the different treatments, there was a trend for the larger fish to enter first more often in sympatry than in allopatry. The tendency for the larger fish in sympatry to enter the shelter first (and so obtain an advantage over intruders) may explain why the largest fish in sympatry was able to monopolise shelter use, regardless of species identity. In contrast, in both allopatric treatments there was a lot of variation in the percentage of times that the large fish entered first, and this may explain why large fish were unable to monopolise shelter use in this situation. Blank & Figler (1996) have previously shown prior residence effects to be important in resolving inter-specific competition for shelters between sympatric red swamp and white river crayfish. Further work is needed to determine the importance of prior residency in determining competitive

advantage for shelter use in Atlantic salmon and brown trout, as the residency effects witnessed in experiment I were established even though fish were introduced to the arena simultaneously.

Evidence from my second experiment, where fish had a choice of habitats, shows that there was a positive relationship between the relative proportion of foraging time that individual fish spent in their favoured deep, slow-flowing water (see chapter 2) and the proportion of sheltering time spent in shelters within that habitat. However, the fact that the relative proportion of foraging time spent in deep water was greater than the equivalent proportion of sheltering time spent in deep-water shelters suggests that fish are willing to move in order to find shelters or foraging habitat. A certain level of activity and continued movement by salmonids in winter may be adaptive in order to avoid periodic flooding, freezing and thaws (Cunjak 1996; Whalen et al. 1999). For instance, Whalen et al. (1999) showed that a period of ice formation led to an extensive alteration in the habitat used by Atlantic salmon parr.

3.5.1 Implications

Intra- and inter-specific competition for shelters (Gregory & Griffith 1996b; this study) can lead to density dependent use of refuge habitat (Armstrong & Griffiths 2001) that could have important implications in terms of the carrying capacity for wild populations of salmonids in streams. In some instances the availability of instream refuges has been found to be high relative to the number of parr, with disturbed individuals being able to find new shelters easily (Cunjak 1988). Such

abundance of shelters relative to the requirements of the population of fish may result in no density-dependent mortality over the winter period (Egglishaw & Shackley 1977; Cunjak et al. 1998). However, in other studies suitable cobble-boulder substrate has been shown to be both limiting (e.g. in areas where the stream flows over the bedrock) and crucial to salmonid survival (Hillman et al. 1987; Griffith & Smith 1993), with individuals emigrating from areas where adequate cover was not available (Bjornn 1971). Under these circumstances, the number of individuals surviving winter may indeed depend on the availability of refuges. In addition to being an important habitat for stream-dwelling salmonids, cobble-boulder substrate has also been shown to be critical to cyprinids (see Cunjak 1996), suggesting that a range of species in temperate streams may compete for the same shelters. Much work is still needed to determine the level of competition between species for shelters in the wild, and the impact that this has on the production of natural fish populations in streams. The impact that shelter competition has is better understood in populations of crayfish, where intra- and inter-specific competition have been shown to be of critical importance in the survival of individuals, particularly the young, through decreased heterospecific predation and cannibalism by conspecifics (Figler et al. 1999). Vorburger & Ribi (1999) also cite competition for shelters as one of the factors that may affect the survival potential of the endangered stone crayfish against invasion from the introduced signal crayfish in Europe.

CHAPTER 4: PRIOR RESIDENCY AND DOMINANCE: THEIR RELATIVE INFLUENCE ON TERRITORY ACQUISITION

4.1 Abstract

In many species where social hierarchy mediates conflict over resources, dominant individuals monopolise food, shelter and reproductive opportunities. The benefits of social dominance, however, can often be offset by a prior residence advantage, whereby individuals arriving first in a new habitat obtain, and subsequently defend, the most profitable sites. The relative influence of these two factors on the acquisition of feeding territories by juvenile Atlantic salmon was investigated by placing groups of six individuals of known dominance rank sequentially into an experimental arena with feeding sites of varying quality. The results show a significant status effect on both the percentage of time spent in a good quality feeding site and individual feeding rate, with dominants having an advantage over subordinates. There was also a significant time of arrival effect, with those individuals that arrive first in a habitat monopolising the resource. The two effects were of approximately equal strength, so that late-arriving dominant fish had similar success to prior resident subordinates. These results indicate that both dominance and prior residence are important in territory acquisition by juvenile Atlantic salmon, and that the two factors can have independent and additive effects.

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4.2 Introduction

Social hierarchies exist in most vertebrate species with dominant individuals able to monopolise scarce resources such as mates, food and safe refuges. Determinants of dominance include size, age, aggressiveness and prior residence (Wilson 1975; Huntingford & Turner 1987). These factors that determine an individual's resource holding potential (RHP) are often directly or indirectly related to one another and it is therefore difficult to separate them and determine the key characteristic (Koivula et al. 1993). For example, in the willow tit dominance is strongly associated with age. However, by independently testing for the effects of body size, age and prior residency on dominance, Koivula et al. (1993) were able to show that the proximate reason for the association between age and dominance in willow tit flocks is the prior residency advantage of the adults. In fish, the earliest fry of Atlantic salmon to emerge from the nest gain a competitive advantage over their later emerging conspecifics by acquiring the available territorial space, but are also larger by the time other fry emerge (Mason & Chapman 1965; Chandler & Bjornn 1988; Metcalfe & Thorpe 1992). In this instance, Cutts et al. (1999a) have since shown that prior residence, and not the size advantage it may subsequently confer, strongly influences which individuals obtain territories.

Prior residents may be most knowledgeable of a territory's value and can subsequently exploit those resources with lower future investment than newcomers, so that they are more prepared to invest energy in territorial contests than new arrivals (Maynard Smith & Parker 1976). Residents may also have a

reduced vulnerability to predators (Metzgar 1967), a greater awareness of established boundaries with neighbours (Beletsky & Orians 1987), and an increased investment in reproductive success (Papaj & Messing 1998). These asymmetries in knowledge between owners and intruders are the basis of the value asymmetry hypothesis of territorial contests (Beletsky & Orians 1989), that has previously found support through experimental studies on birds (Krebs 1982; Tobias 1997) and fish (Johnsson et al. 2000; Nijman & Heuts 2000). Johnsson et al. (2000) provided supportive evidence by showing that juvenile brown trout territory owners invested more resources in defence of preferred habitats than did owners of non-preferred habitats. Papaj & Messing (1998) have shown that it is not only the value of a resource that influences the resident's willingness to expend energy defending it, but also the resident's prior use of the resource and physiological condition, in this case reproductive status. The occupation of a territory can have profound effects on an individual's fitness and life-history strategy. For instance, juvenile salmon with prior residence advantage grew faster and so had a higher chance of smolting (transformation to the seaward migration phase of the life cycle) in their first year than those without prior residence (Metcalfe & Thorpe 1992; Cutts et al. 1999a). Moreover, emerging salmonids that fail to establish territories are forced to emigrate downstream and mortality for these individuals can be high (Elliott 1990).

Early-emerging salmon fry differ from their later emerging conspecifics, in that they tend to have higher metabolic rates which, while costly in some circumstances, are linked to more aggressive, dominant behaviour (Metcalfe et al. 1995). However, O'Connor et al. (2000a) found that the advantage gained by

emerging early cannot be completely attributed to intrinsic differences in dominance and was partly mediated by a prior residence effect. Moreover, the importance of the interaction between prior residence and dominance is likely to arise at various points throughout the life-histories of juvenile salmonids, since the optimum stream microhabitats for feeding territories change with body size and season, so necessitating movements within the river system. In addition to an upstream migration in summer (Armstrong et al. 1994) and a switch to new habitats in autumn (Rimmer et al. 1983), hydrological disturbances such as spates or droughts, or escape from a predator can force some individuals out of the areas with which they are familiar (Armstrong et al. 1997).

Beaugrand et al. (1991, 1996) have studied the interactions between size, prior residence and prior social experience in determining the outcome of territorial contests in green swordtail fish. They report that the key factor in determining the outcome of contests depended on the size difference between opponents. When large size asymmetries existed, size uniquely determined dominance outcome, whereas when size asymmetries were small, prior residence and prior experience became more important. In the case of salmonids, Huntingford & García de Leániz (1997) have previously studied the relative effects of prior residence and dominance, but not at the critical stage of early emergence when mortality is at its peak. In this study I use an experimental approach to examine the interaction between prior residence and dominance in similar sized Atlantic salmon fry competing for feeding sites. By measuring relative dominance status in the absence of a prior residence asymmetry and then manipulating the order of entry into the habitat according to intrinsic dominance status, I tease apart the

independent contributions that intrinsic status and prior residence have on competitive ability. This allows assessment of the extent to which a territory holder's prior residence advantage can be over-ridden by a more dominant later arrival.

4.3 Methods

4.3.1 Subjects

The subjects of these experiments were underyearling offspring of sea-run salmon caught in the River Almond, Perthshire, U.K. They were raised at Almondbank Hatchery, Perthshire, U.K. and transferred to the University of Glasgow, U.K. for testing. The fish (fork length = 34.1 ± 0.14 mm (mean ± standard error (S.E.)); weight = 0.32 ± 0.005 g) were held in a tangential-flow tank where they were fed frozen chironomid larvae (bloodworm), except when being tested.

4.3.2 Stream tanks

Experiments were carried out in a flume system comprising a stack of three glass tanks each measuring 180 x 25 x 20 cm and one glass tank measuring 120 x 25 x 20 cm, all of which were interconnected by plastic pipes. These tanks then drained into two 60-litre sumps from which water was recirculated by pumping it to the top flume tank. The water flowed through the glass tanks at approximately 0.08 $m \cdot s^{-1}$. The tanks had a 2 cm layer of gravel as a substrate and a water depth of 13 cm. Partitions placed within the glass tanks created compartments;

the partitions were opaque but had panels of fine mesh to allow a directional current through the tanks. Three sizes of compartment were used in the experiment: arenas where dominance testing was carried out measured 40 x 12.5 cm, whereas those used to hold fish removed from dominance trials measured 20 x 12.5 cm. Experimental arenas measured 60 x 12.5 cm, and contained six evenly-spaced feeders. These were 25 ml universal tubes with a small hole near the top to allow water to circulate, and a small hole (1.5 mm in diameter) near the bottom to allow live chironomids to crawl out at random times after having been placed in the feeder. Each universal tube was held by a plastic mount so that the exit hole for the chironomids was 5.5 cm above the substrate.

In order to create feeding sites of varying quality, and so induce competition, the feeders were given contrasting food supplies: the two middle feeders received four chironomid larvae per day, those directly adjacent to these received two per day, while those at the very front and back of each experimental arena received no chironomids at any point during the experiment. Food was delivered at 11.30 and 15.00 on each day of the experiment and equal amounts of food were given in the morning and afternoon.

4.3.3 Dominance testing

Fish were individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anesthetisation using benzocaine. Replicate groups of six size-matched fish were then placed in dominance testing arenas and allowed to recover overnight. The following day, fish were fed by placing an

individual chironomid at the upstream end of the testing arena using a pipette. This procedure was repeated at regular intervals throughout the day to allow the fish to acclimatise to the new tank surroundings and feeding technique. This feeding protocol was used in all future dominance trials. Following the day of training, fish were tested for dominance status over the following three days in a manner similar to that used by Metcalfe et al. (1989). On each day, at 45-minute intervals, a single chironomid was released at the upstream end of each testing arena and the fish scored on their initial position in the tank and their ability to compete for the food item. Ten chironomids were delivered in this way and then the scores were added for each fish. Points were awarded as follows:

+1 for holding the most profitable location in the testing arena defined as the nearest central position downstream of where the chironomids were released,

+1 for obtaining an uncontested food item,

+2 for obtaining the food if the item was contested by another fish.

The individual with the highest overall score for that day was defined as the most dominant fish in the group, and was removed and placed in the holding arena. If two fish had scores within five points of each other after ten repetitions, then testing continued until there was a five point or greater difference. After removal of the dominant the other fish were fed to excess and left overnight. They were then tested as above to find the most dominant of the remaining fish. Three days of dominance testing allowed us to define the three more dominant and three more subordinate fish in each group of 6.

4.3.4 Experimental procedure

These same groups of six fish of known rank were then used in the main experiment under three different treatments, designed to test for the relative influence of dominance and prior residence on territory acquisition. The three treatments were as follows:

1. Three subordinates placed in the experimental arena for three days, with the three more dominant fish being added on the evening of day 3.
2. Three dominants placed in the experimental arena for three days, with the three subordinate fish being added on the evening of day 3.
3. All six fish placed in the experimental arena simultaneously.

Fish were placed in their experimental arena on the evening of the last day of dominance testing and observations began the following day. Those fish that were not to enter the experimental arena until the evening of day 3 were kept in the holding arena and fed three live chironomids per fish per day. This procedure ensured that all fish maintained a similar level of feeding motivation.

The position of each fish in each experimental arena was recorded at 10.00, 11.30, 13.30 and 15.00 each day. Fish holding position in front of all six feeders were given a value of 0. For each fish holding position at a feeding station I recorded which feeder it was nearest to. Observations of feeding behaviour and aggressive interactions were made over a five-minute period at 11.30 and 15.00, immediately after the feeders had been replenished. Feeding behaviour was logged by recording the number of successful feeding attempts by each fish. For all aggressive interactions the initiator and recipient were noted along with the

nature of the aggressive interaction, classified as being either a display, chase, charge or nip (see Keenleyside & Yamamoto 1962 for a description of aggressive behaviour in juvenile salmon).

These observations were maintained for five days, and each of the three treatments was repeated eight times between the 27th May and 27th June 2000. However, in one replicate of treatment 3, where all six fish were added simultaneously, three fish died and thus this replicate was not included in the analysis. Trials were carried out at ambient light and temperature levels for that time of year. Water temperature was recorded daily and varied between 11.7 and 13.1 °C over the course of the experiment.

4.3.5 Data analysis and statistical treatment

To determine whether there was any effect of size on the social status obtained by individual fish, I used a paired t-test to compare the mean length of the three dominants with that of the three subordinates in each replicate of each treatment. In the main experiment, three behavioural properties were of greatest interest: the spatial positions adopted by individual fish, their feeding rate and their aggressive behaviour. I quantified position in the tank by calculating the percentage of time that each individual fish spent in a good quality site, this being defined as any of the four feeding stations that received chironomid larvae. Feeding behaviour was quantified by counting the number of successful feeding attempts by each fish in the ten five-minute observation periods, and expressing this as a feeding rate per minute. Aggression was calculated for each fish as the

number of wins it achieved as a percentage of the number of aggressive encounters in which it was involved. The percentage of aggressive interactions that were displays as opposed to more overt aggression (chases, charges and nips) was also calculated. Separate values were calculated for each behaviour on days 1-3 and 4-5 of the experiment (i.e. before and after introduction of the second wave of fish in treatments 1 and 2). The change in behaviour between days 1-3 and 4-5 was also calculated by subtracting an individual's behavioural score for days 1-3 from its score for days 4-5.

Having obtained behavioural scores on days 1-3 and 4-5 for the dominants and subordinates in each replicate of each treatment, I then analysed the data in the following way. In all cases, the mean values of the three dominant and three subordinate fish in a replicate were used as the data points so as to preserve statistical independence (i.e. n = number of replicates). Analysis of covariance (ANCOVA) was used with position, feeding, or aggression won as the dependent factor, and status (dominant or subordinate) and time of arrival as fixed factors. This was done separately for days 1-3 and 4-5 in order to determine the influence of status and time of arrival on behaviour patterns. Repeated measures analysis of variance (ANOVA) was then used to analyse any change in behaviour between days 1-3 and 4-5, with date (days 1-3 or 4-5) as the within-subject factor and status and time of arrival as between-subject factors. An independent samples t-test was performed to compare the average change in behaviour when adding more subordinate fish to a resident group of dominants, with the average change in behaviour when adding more dominant fish to a group of resident subordinates. A paired samples t-test was also carried out to see if there was any

difference in the change in behaviour between dominants and subordinates for days 1-3 and 4-5, when all fish were added simultaneously. All percentage data were normalised by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for two-tailed tests of significance.

4.4 Results

4.4.1 Influence of size on dominance status

There was no significant effect of length on social status (possibly because size differences within groups of fish were minimised), although there was a trend for dominants to be larger than the subordinates in their group (paired samples t-test: $t_{22} = 1.95$, $P = 0.064$; dominants: fork length = 34.3 ± 0.31 mm (mean ± standard error (S.E.)); subordinates: fork length = 33.8 ± 0.28 mm).

4.4.2 Percentage time spent in good quality sites

On days 1-3 of the experiment there was no significant effect of status or time of arrival (which indicates whether all six or only three fish were added on day 1) on the percentage of time spent in good quality sites (see Table 4.1). However, there was a noticeable trend for dominant fish to spend more time in a good site than subordinates when the groups were added simultaneously (see Fig. 4.1a). In contrast, by days 4-5 there were significant effects of both status and time of arrival on the percentage of time that fish spent in good quality sites (Table 4.1). Figure 4.1b shows that dominant fish spent a greater proportion of their time in good sites than subordinates, and fish that arrived first spent a greater percentage

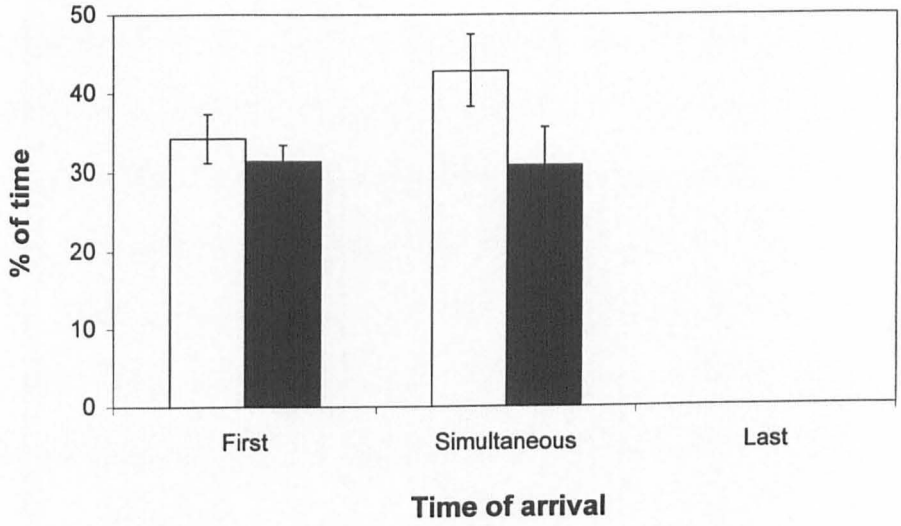
Table 4.1. Summary of the results from a series of analyses of variance to determine the influence of status (dominant or subordinate) and time of arrival (day 1 or day 4) on behavioural responses (dependent factors). Analyses were conducted separately for days 1-3 (when 'time of arrival' indicates whether all six fish or only three fish were added on day 1) and days 4-5.

Source of variation	d.f.	F	P
Percentage time spent in a good quality site			
Days 1-3			
Status	1,26	4.08	0.054
Time of arrival	1,26	1.21	0.281
Status * time of arrival	1,26	1.52	0.228
Days 4-5			
Status	1,40	9.10	0.004
Time of arrival	2,40	3.87	0.029
Status * time of arrival	2,40	1.64	0.207
Feeding rate			
Days 1-3			
Status	1,26	1.11	0.303
Time of arrival	1,26	52.42	< 0.001
Status * time of arrival	1,26	0.75	0.395
Days 4-5			
Status	1,40	22.41	< 0.001
Time of arrival	2,40	20.34	< 0.001
Status * time of arrival	2,40	2.05	0.142

Table 4.1. continued

Source of variation	d.f.	F	P
Percentage of aggressive encounters won			
Days 1-3			
Status	1,25	2.27	0.145
Time of arrival	1,25	5.69	0.025
Status * time of arrival	1,25	0.67	0.420
Days 4-5			
Status	1,39	< 0.01	0.944
Time of arrival	2,39	12.68	< 0.001
Status * time of arrival	2,39	1.08	0.351
Percentage of aggressive interactions that were displays			
Days 1-3			
Status	1,25	0.10	0.755
Time of arrival	1,25	10.09	0.004
Status * time of arrival	1,25	0.64	0.430
Days 4-5			
Status	1,33	1.40	0.245
Time of arrival	2,33	0.56	0.576
Status * time of arrival	2,33	0.43	0.654

a)



b)

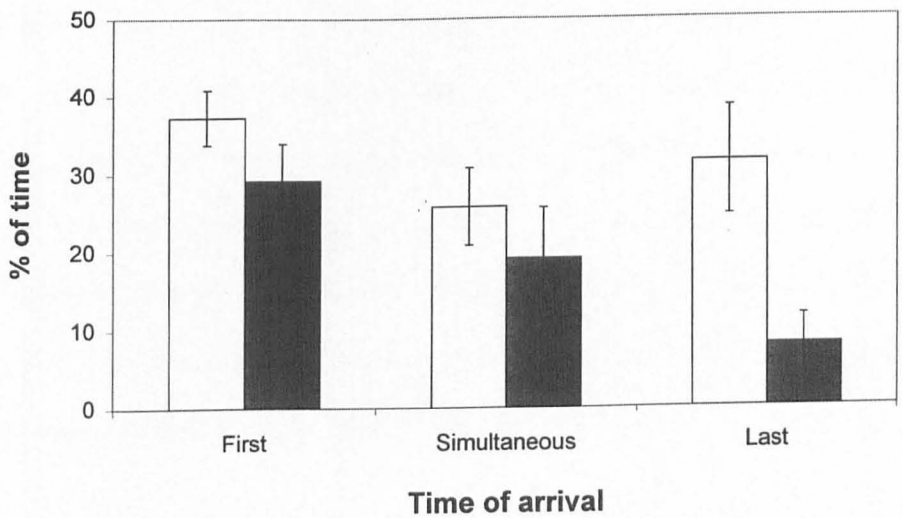


Figure 4.1. Percentage of time (arcsine-transformed ± SEM) spent at good quality feeding sites for dominants (open bars) and subordinates (shaded bars) under different treatments on a) days 1-3 and b) days 4-5. Note that dominants in the 'First' treatment would have been in the same tank as subordinates in the 'Last' treatment.

of time in good sites than fish that arrived simultaneously or last. Repeated measures ANOVA to compare the percentage of time spent in a good site on days 1-3 with days 4-5, revealed a significant date effect (Table 4.2) with fish spending less of their time in a good quality site on days 4-5 than they did on days 1-3 (see Figs 4.1a & b). This analysis also shows a significant interaction between date and time of arrival, with date having less of an effect on fish given a prior residence advantage than those that arrived simultaneously. The significant between-subject status effect confirms that dominant fish spent greater percentages of their time in good quality sites than did subordinate fish.

There was no significant difference between the average change in percentage of time that resident subordinates spent in a good site when more dominant fish were added, and the equivalent change in use of good sites by resident dominants when subordinates were added (independent samples t-test: $t_{14} = 0.75$, $P = 0.468$). There was also no significant difference between dominants and subordinates in the change between days 1-3 and 4-5 in the percentage time spent in a good site when all fish were added simultaneously (paired samples t-test: $t_6 = 0.61$, $P = 0.562$), confirming that the observed changes in the other treatment groups were not simply due to temporal changes in behaviour.

4.4.3 Feeding rate

On days 1-3 of the experiment there was no significant status effect on feeding rate. However, there was a significant time of arrival effect, with fish in treatments where only three fish were present on days 1-3 having (not

Table 4.2. Summary of a series of repeated measures ANOVAs to test for the effects of date (within-subject factor: classified as days 1-3 versus days 4-5), status (dominant or subordinate) and time of arrival (first or simultaneous) on behavioural responses of fish added on day 1.

Source of variation	d.f.	F	P
Percentage time spent in a good quality site			
Within-subjects			
Date	1,26	7.29	0.012
Date * status	1,26	< 0.01	1.000
Date * time of arrival	1,26	8.29	0.008
Date * status * time of arrival	1,26	1.04	0.317
Between-subjects			
Status	1,26	4.42	0.045
Time of arrival	1,26	0.90	0.353
Status * time of arrival	1,26	0.29	0.592
Feeding rate			
Within-subjects			
Date	1,26	0.30	0.588
Date * status	1,26	11.42	0.002
Date * time of arrival	1,26	2.24	0.146
Date * status * time of arrival	1,26	0.94	0.342
Between-subjects			
Status	1,26	14.56	0.001
Time of arrival	1,26	44.59	< 0.001
Status * time of arrival	1,26	0.03	0.864

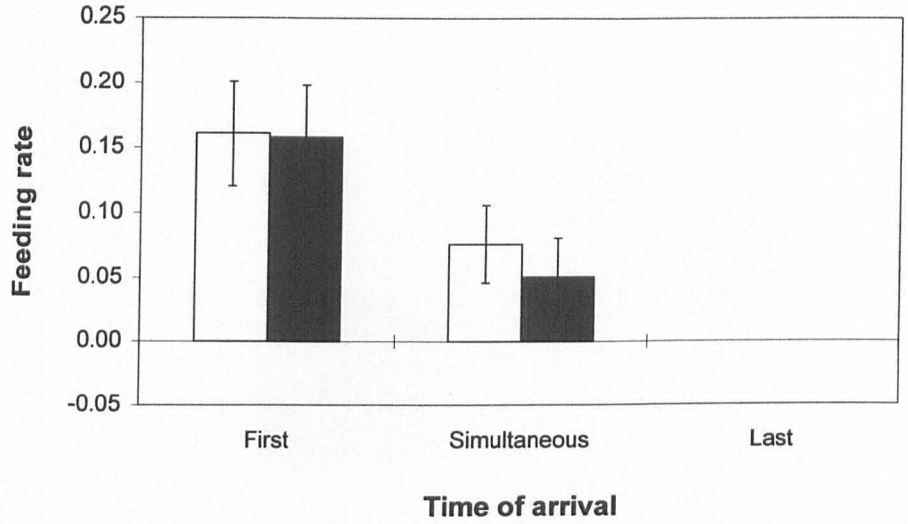
Table 4.2. continued

Source of variation	d.f.	F	P
Percentage of aggressive encounters won			
Within-subjects			
Date	1,24	0.35	0.558
Date * status	1,24	3.25	0.084
Date * time of arrival	1,24	0.11	0.739
Date * status * time of arrival	1,24	1.18	0.299
Between-subjects			
Status	1,24	0.07	0.793
Time of arrival	1,24	7.79	0.010
Status * time of arrival	1,24	0.03	0.874

surprisingly) significantly higher feeding rates than those when six fish were added simultaneously (Table 4.1; Fig. 4.2a). This time of arrival effect on feeding rate was also evident on days 4-5 of the experiment, with fish arriving first obtaining significantly more food than those arriving either simultaneously or last (Table 4.1; Fig. 4.2b). There was also a significant status effect on days 4-5, with dominants acquiring significantly more food than subordinates at all arrival times (Table 4.1; Fig. 4.2b). The repeated measures ANOVA to compare feeding behaviour between days 1-3 and days 4-5 revealed no significant date effect (Table 4.2; Figs 4.2a & b). However, there was a significant date by status interaction (Table 4.2), indicating that the effect of date depended on the status of the fish. Comparison of Figure 4.2a & b reveals that date had less effect on the feeding rate of dominant than on subordinate fish, with only the latter showing a marked decrease in food intake rate on days 4 and 5. The significant effects of status and time of arrival (Table 4.2) confirm the advantage conveyed by dominance and early arrival on the acquisition of food seen in the analysis of covariance results.

There was a significant difference between the average change in feeding rate of resident subordinates when more dominant fish were added, and the equivalent change in feeding rate by resident dominants when subordinates were added. This was due to a greater reduction in the feeding rate of subordinates when adding more dominant fish, than there was when more subordinate fish were added to a group of resident dominants (independent samples t-test: $t_{14} = 3.19$, P = 0.007; Fig. 4.3). There was no significant difference between dominants and subordinates in the change in the rate of feeding on days 1-3 and days 4-5 when

a)



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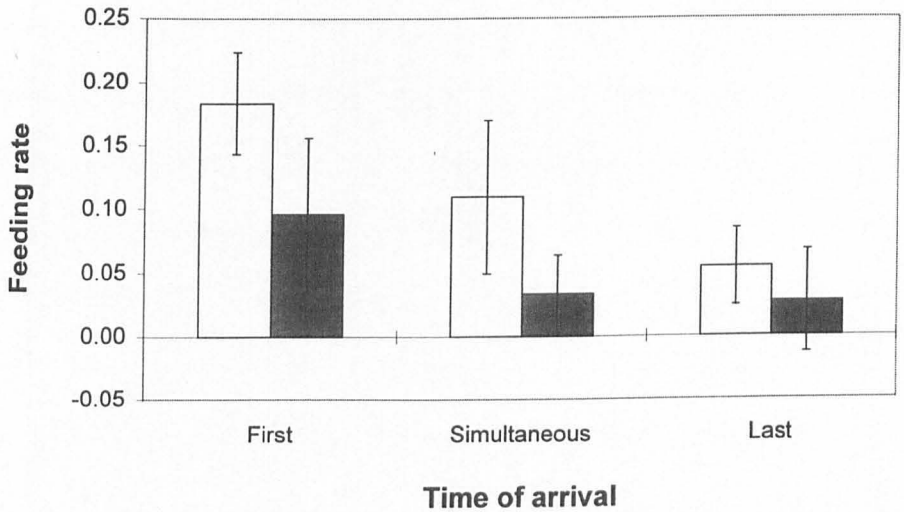


Figure 4.2. Average feeding rate (min^{-1} ± SEM) for dominants (open bars) and subordinates (shaded bars) under different treatments on a) days 1-3 and b) days 4-5.

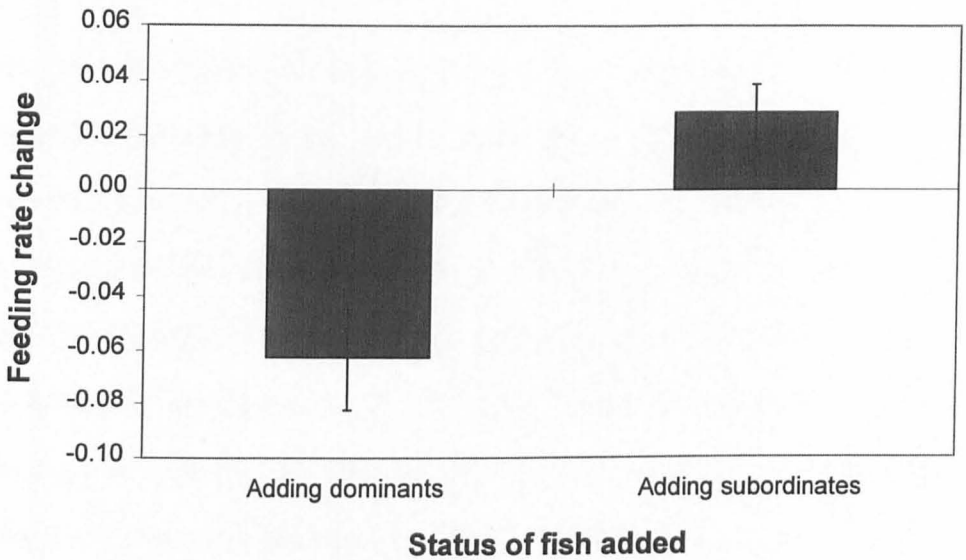


Figure 4.3. Change in feeding rate (min^{-1} ± SEM) from days 1-3 to days 4-5 for resident subordinates when adding more dominant fish, and for resident dominants when adding more subordinate fish.

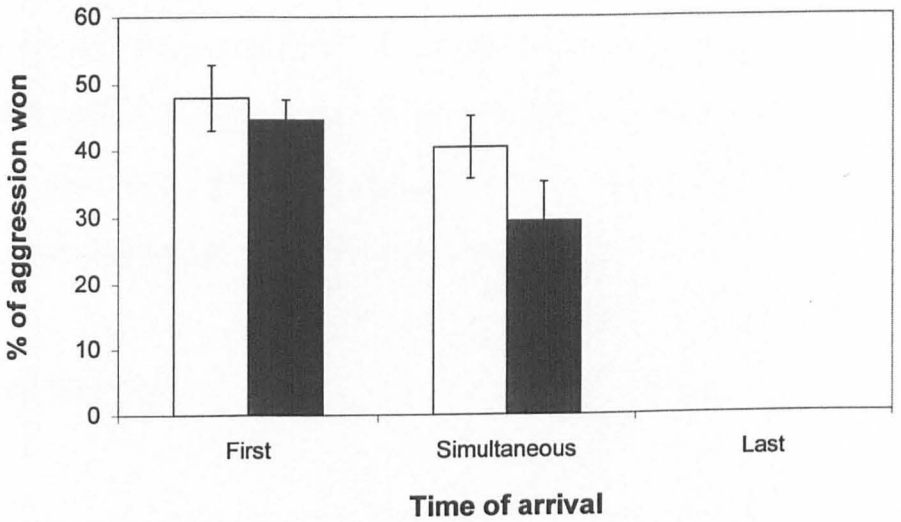
all fish were added simultaneously (paired samples t-test: $t_6 = 1.71$, $P = 0.139$).

4.4.4 Aggression

There was no significant effect of status on the percentage of aggressive interactions won either on days 1-3, or on days 4-5 (Table 4.1; Figs 4.4a & b). There was, however, a significant time effect both on days 1-3 and days 4-5, indicating that fish arriving first won a significantly higher percentage of aggressive encounters than fish arriving simultaneously or last (Table 4.1; Figs 4.4a & b). The repeated measures ANOVA revealed no significant change in the percentage of aggressive encounters won on days 1-3 compared with days 4-5 (Table 4.2). There was, however, a significant between-subjects effect of time of arrival (Table 4.2), confirming that fish arriving first won significantly more interactions than those arriving simultaneously or last. There was no significant difference between the average change in percentage of aggressive encounters won by the residents when adding more dominant fish to a group of subordinates, than there was when adding more subordinate fish to a group of dominants (independent samples t-test: $t_{13} = 0.40$, $P = 0.968$). There was also no significant change between days 1-3 and 4-5 in the percentage of aggressive encounters won by dominants and subordinates when all fish were added simultaneously (paired samples t-test: $t_5 = 1.16$, $P = 0.300$).

There was no significant effect of status on the percentage of aggressive interactions that were displays, as opposed to more overt aggression, when all fish were added simultaneously (paired samples t-test: $t_6 = 0.79$, $P = 0.940$).

a)



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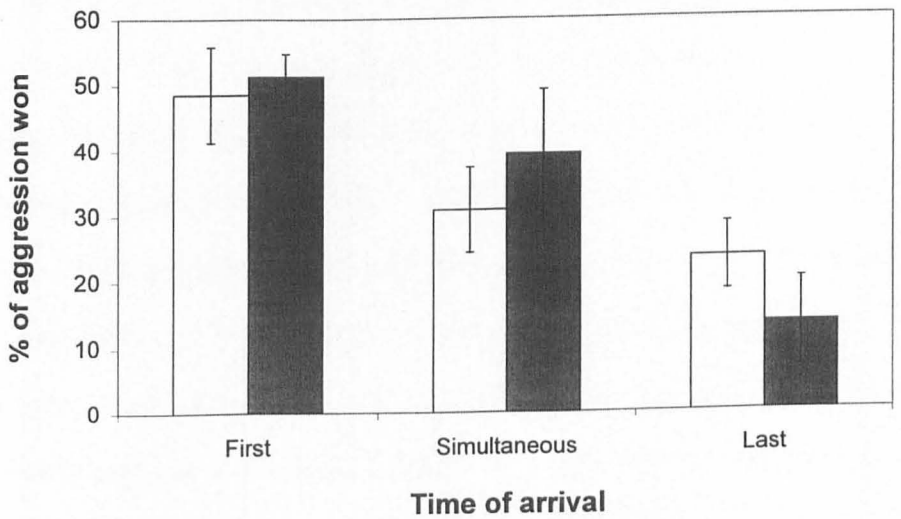

Figure 4.4. Percentage of aggressive encounters won (arcsine-transformed ± SEM) for dominants (open bars) and subordinates (shaded bars) under different treatments on a) days 1-3 and b) days 4-5.

When considering all the treatments, there was also no status effect on the percentage of aggressive encounters that were displays on days 1-3 or on days 4-5 (Table 4.1). There was, however, a significant time of arrival effect on days 1-3 (Table 4.1), with there being a greater percentage of displays in treatments where only three fish were present on the first three days, as opposed to treatments where all six fish were added on day 1.

4.5 Discussion

The trend for dominants to spend a greater percentage of time in good quality sites, and to acquire more food than subordinates when all six fish were added simultaneously, is consistent with the general phenomenon that dominant individuals gain priority access to food (e.g. Gill & Thomson 1956; Murton et al. 1966; Fausch 1984). A comparison of feeding rates on days 1-3 and days 4-5 reveals that there was no significant difference between dominants and subordinates on the first three days, but there was a clear distinction on the last two days of the experiment. This arises because the feeding rate of subordinates decreased from days 1-3 to days 4-5, whereas that of dominant fish slightly increased. These temporal changes in feeding rate suggest that the advantage dominants hold over subordinates in terms of food acquisition is not immediate upon entry into a new habitat, and can take several days to develop. The duration of this period when dominants feed at a lower rate than their potential is a measure of the 'settlement cost', and has previously been witnessed in European robins (Tobias 1997). Tobias reported that newcomers to a territory where the resident had recently been removed allocated more time to singing (i.e.

advertising ownership) and less time to foraging than established territory holders. Furthermore, the time taken for dominance status to be conferred on newcomers corresponded to the length of time it took for the singing and foraging levels of the intruder to return to average levels for the population. In my study, it is likely that dominants gained no immediate advantage over subordinates in terms of feeding rate because they devoted more time to defence or assessment of the feeding sites, rather than feeding. It is not uncommon for a resident to expend energy on defending a resource and yet gain no immediate benefits. For example, in species where males defend breeding territories, the advantage gained by holding a good site may take months to be realised (e.g. Yasukawa 1980; Currie et al. 2000).

Despite there being no advantage to dominants in terms of feeding rate over the first three days of the experiment, dominants did have an advantage over subordinates in the amount of time spent in a good site. Although there was no significant status effect on the percentage time in a good site on days 1-3, this was due to the fact that when added to separate arenas, dominants and subordinates spent the same percentage of time in good sites. Both dominants and subordinates greatly reduced their percentage of time in good sites on days 4-5 compared to days 1-3. Despite this reduction, dominants still spent a greater percentage of time in good quality sites on days 4-5 than did subordinates. Dominants may have reduced their percentage time in a good site over the course of the experiment because, having established their superior status, the most profitable position was often at the back of the arena. Although this site received no chironomids at any stage of the experiment, water flow through the arena

meant that it was often easiest to see and capture prey from a position near the back of the arena. Although subordinates also congregated there, the dominant fish were always in more upstream positions and thus occupied the best feeding positions, without necessarily holding position in a site that received food. Cutts et al. (1999a) observed similar behaviour, with individuals of higher rank spending significantly longer at the upstream end of a group of non-territorial fish than more subordinate individuals.

This feature of the experimental set-up may also explain why on average, neither dominants nor those given a prior residence advantage spent greater than 50% of their time in good quality sites, despite there being roughly equal areas of 'good' and 'poor' feeding sites. The fish were not holding individual territories, despite using an arena that should, based on territory sizes previously observed (see Grant & Kramer 1990 and references therein), have allowed at least three fish to defend individual territories. One would have also expected territory sizes to be smaller than in open stream tanks because of the visual isolation conferred by the plastic mounts holding the feeders (see Kalleberg 1958).

The significant effect of arrival time on feeding rate over the first three days of the experiment is likely to be caused by the varying number of fish within each treatment. As the 'time of arrival' term in the analyses based on data from days 1-3 actually reflects the number of fish present, with all six present in the simultaneous treatment but only 3 in the other two treatments, it is logical that fish in treatments with only three fish present achieved higher feeding rates than those where six fish were present. However, when testing for time of arrival

effects on the last two days of the experiment (when all treatments had the same number of fish present), there were clear advantages to prior residence in terms of both feeding rate and the percentage of time spent in good quality sites. The reward for arriving first in a habitat was that individuals were able to maintain a high percentage of time in a good quality site throughout the course of the experiment. In contrast, in the treatment where all six fish were added simultaneously, both dominants and subordinates spent less time in good quality sites on the last two days than they did over the first three days of the experiment.

The feeding rate of subordinates given a prior residence advantage did decrease over the course of the experiment, but not to the same extent as subordinates arriving simultaneously with five other fish or those arriving last. Dominants that were also given a prior residence advantage were able to maintain their feeding rate over the course of the experiment. The interaction between prior residence advantage and dominance was also witnessed when adding more dominant fish to a group of resident subordinates, in comparison to adding a group of more subordinate fish to a group of resident dominants. The arriving group of more dominant fish was able to force a greater reduction in the feeding rate of residents than the arriving group of subordinates, highlighting the importance of social status. This result suggests that higher status intruders can potentially overcome the advantage of prior residence. Other studies have found that the interaction between prior residence and dominance in determining resource acquisition is dependent on the nature of the two opponents. For example, Beaugrand et al. (1996) showed that prior residence only conveyed an

advantage to male green swordtail fish when both opponents had experienced defeat prior to meeting and size asymmetries were small. In contrast, Baugh & Forester (1994) found that resident dart poison frogs were consistently dominant over intruders, irrespective of the intruder's size. Prior residence advantage is also not superseded by size in green frogs (Wells 1978) or harlequin frogs (Crump 1988). However, size has been shown to be more important than prior residency in female shrimps (Evans & Shehadi-Moacdieh 1988), convict cichlids (Wazlavek & Figler 1989) and the bullfrog (Emlen 1976). This disparity in outcomes may result from a number of factors such as the extent to which relative body size correlates with dominance status, the value of the resource in contention (Baugh & Forester 1994), or the time allowed to settle on the territory (Tobias 1997). This latter suggestion may be a factor in my study, and one might expect that if relatively subordinate fish had been given a longer settling time, then their feeding rate may not have decreased as much on addition of more dominant fish. However, this is unlikely to be the case as Huntingford & García de Leániz (1997) have previously demonstrated that one day was sufficient for a prior residence effect to be evident in Atlantic salmon parr. Behavioural differences between species may also be important in explaining the range of results obtained. For instance, Chellappa et al. (1999) found that prior residence was the key determinant of the outcome of territorial contests in male freshwater angelfish, whilst Turner (1994) found that prior residence can be overriden by a size advantage in male mouth breeding cichlids. Chellappa et al. (1999) suggest this variation could be due to differences in habitat preferences, and that in the dense vegetation where angelfish defend territories, relative size may be more

difficult to assess than in the open areas where mouth breeding cichlids are found.

The highly synchronous emergence pattern of offspring salmonids from a nest (Gustafson-Marjanen & Dowse 1983), as with dispersing young of some other species (e.g. cicadas, reviewed in Krebs & Davies 1993), is generally explained by the dilution effect, with individuals emerging at the same time being less likely to fall victim to predation (Brännäs 1995). However, there are other conflicting evolutionary pressures acting on emergence time. For instance, harsh climatic conditions early in the season select for late-emergence (e.g. Crecco & Savoy 1985), whilst in populations that compete for limited resources such as territories, early emergence is selected for since latecomers will be at a competitive disadvantage that may not be completely over-ridden by intrinsic status (e.g. Cutts et al. 1999b; Johnsson et al. 1999; this study). Variability between individual systems is also likely to sustain a range of emergence traits. For example, Einum & Fleming (2000) provide evidence for selection for early emergence, with one of the main factors being that late-emergers are displaced downstream by aggressive behaviour by juveniles that were already settled on available territories. This displacement of those emerging late increased their predator-encounter rates since adult brown trout were prevalent in the lower, deeper reaches of the river system.

In the majority of species, aggression mediates conflict over resources, with the level of aggression being positively correlated with dominance (Huntingford & Turner 1987). However, although individuals given a prior residence advantage

initiated and won a significantly higher percentage of interactions than fish arriving either simultaneously or last, fish previously categorised as dominants and subordinates did not differ in the level of aggression they won. Aggression was not directly measured during the dominance trials, which might give rise to the concern that fish were classed as dominants and subordinates depending on their motivation to feed rather than any true indication of social status. However, dominant and subordinate fish added to separate arenas on day 1 fed at equal rates over the first three days of the experiment, indicating that their motivation to feed was similar. There are several other possible explanations for this unexpected similarity in the level of aggression won by dominants and subordinates. Firstly, the aggression observed may not have been related to the establishment of rank, because fish had already resolved their position in the social hierarchy during the dominance trials. This theory is supported by the fact that salmonids have previously been shown to be able to resolve contests quickly (O'Connor et al. 1999), with dominance hierarchies forming within a 24-hour period (e.g. Metcalfe et al. 1989). Secondly, once a dominant had attained the best area, the onus would be on the other individuals to fight for that space. Therefore, subordinates could be expected to be as aggressive as dominants. This would be particularly important at the time of early settlement, because the costs of failing to compete effectively for food at the fry stage are starvation and death (Elliott 1990), whereas later in life the costs of subordinance may not be quite as severe. Related to both these points is the possibility that because observations were made immediately after the feeders were restocked all fish became more aggressive at these times, but that when initially competing for

access to feeding sites dominants won significantly more aggressive interactions than subordinates.

These results highlight the advantages of both prior residence and social dominance. Their effects were additive, with dominants being able to increase their fitness even further by arriving first in a new habitat. Prior residence and dominance were also shown to act independently, as previously shown by Huntingford & García de Leániz (1997), with subordinates able to gain a prior residence advantage if they arrived early. There is some evidence in the current study that the effects of social dominance may be able to override a prior residence advantage of a subordinate. However, individuals would have to be monitored for a longer period of time and growth rates examined to be able to confirm this. In contrast, there are some species in which prior residence is strong enough to override size and age effects on dominance (e.g. marsh tits, Nilsson 1989; willow tits, Koivula et al. 1993). In such circumstances, early arrival and settlement provides a viable alternative to overcome intrinsic disadvantages in terms of size, age or aggressiveness. By arriving early and gaining a prior residence advantage individuals can increase their resource holding potential (RHP). Winner-loser effects by which prior experience of winning increases the likelihood of success in further bouts (Huntingford & Turner 1987; Beaugrand et al. 1991, 1996) may then increase an individual's RHP further.

CHAPTER 5: THE INFLUENCE OF PRIOR RESIDENCE ON THE ABILITY TO RETAIN A TERRITORY IN ATLANTIC SALMON FRY

5.1 Abstract

The influence of prior residence on the ability of Atlantic salmon fry to defend a food resource was investigated in a laboratory flume system. Groups of three individuals were given a prior residence advantage by allowing them exclusive use of a food resource for two days. The behaviour of these fish on release into an experimental arena containing three identical feeding sites was compared with groups of three individuals that arrived simultaneously. I test the four specific hypotheses that prior resident individuals were: 1) more site-attached; 2) fed more from the site in which they were resident; 3) more aggressive and 4) better able to exclude intruders from their territory. The behaviour of prior residents did not differ significantly from fish added simultaneously to the arena in the extent to which they were site-attached, the positions from which they fed or their ability to exclude intruders from their feeding site. However, prior resident fish were significantly more aggressive than individuals that arrived simultaneously. These results suggest that the period of site residence influenced fish behaviour but that the spatial and temporal unpredictability of the food resource resulted in prior residents gaining no advantage over those that arrived simultaneously.

5.2 Introduction

Animals spend their time within home ranges, regions within which they carry out their normal activities and obtain enough food, water, shelter and mating opportunities in order to survive and reproduce (Goodenough et al. 1993). Within this home range, many animals hold territories, areas that they defend more or less exclusively (but see Schoener 1968), in order that they may monopolise the resources within that area (see Wilson 1975; Grant 1997). Competition for territories can be intense, particularly during times of year when resources are scarce, such as during the breeding season when individuals compete for mates and nests, or during winter when food is often limited. Territoriality is a common phenomenon, particularly among birds (Oring 1982) and to a lesser extent fish (Grant 1997). The importance of territories to many species has led to research on the impact that territory ownership can have on breeding success (e.g. Bollmann et al. 1997; Currie et al. 2000; Pärt 2001) and survival (e.g. Elliott 1990).

The factors influencing an individual's ability to acquire and maintain a territory has been the focus of research on many animal groups. For example, Kemp (2000) studied the effects of age and size on territorial contests in a tropical butterfly. Other factors known to influence territorial contests are aggressiveness and prior residence (e.g. Baugh & Forester 1994; Blank & Figler 1996; chapter 4). Prior residence of an area can confer an advantage that can override intrinsic differences in size or fighting ability (e.g. Wells 1978; Yasukawa & Bick 1983; Baugh & Forester 1994). Such an advantage can have serious implications for

future fitness as it can lead to higher growth rates (Huntingford & García de Leániz 1997; O'Connor et al. 2000a), more copulations (e.g. Haley 1994) and a competitive advantage both within and between species (e.g. Glova & Field-Dodgson 1995; Cutts et al. 1999a,b). There are various explanations as to why such a prior residence advantage may arise. Firstly, a resident may know the value of a resource better than an intruder and therefore be more willing to invest energy in territorial contests than newcomers (Krebs 1982; Beletsky & Orians 1989). Alternatively, intruders may be sizing up a number of residents before engaging in conflict with one territory owner, and may therefore withdraw from many contests before they escalate (Grafen 1987).

In this chapter I concentrate on the effect that a prior residence advantage has on the ability of Atlantic salmon fry to defend and retain a territory. Kalleberg (1958) and Keenleyside & Yamamoto (1962) first reported territorial behaviour in salmonids. They described the interactions between individual Atlantic salmon and brown trout aggressively defending territories from intruders. Subsequently, Fausch (1984) suggested that the ideal territory for such sit-and-wait predators (see Stradmeyer & Thorpe 1987) was a location at which an individual can maintain position within slow-flowing water, thus minimising energy expenditure, but adjacent to an area of fast-flowing water, thus maximising feeding opportunities. Whilst there has been some debate on how exclusive salmonid territories are (see Bachman 1984), territorial behaviour among groups of salmonids has been observed both with respect to feeding sites (e.g. Kalleberg 1958; Fausch 1984) and shelter (Gregory & Griffith 1996b; chapter 3). I test the specific hypotheses that prior resident individuals were 1)

more site-attached; 2) fed more from the site in which they were resident; 3) more aggressive and 4) better able to exclude intruders from their feeding site.

5.3 Methods

5.3.1 Subjects

The subjects of these experiments were underyearling offspring of sea-run salmon caught in the River Almond, Perthshire, U.K. They were raised at Almondbank Hatchery, Perthshire, U.K. and transferred to the University of Glasgow, U.K. for testing. The fish (fork length at the time of testing = 37.2 ± 0.36 mm (mean ± standard error (S.E.)); weight = 0.47 ± 0.02 g) were untested individuals from the same stock as those used in chapter 4. They were held in a tangential-flow tank where they were fed frozen chironomid larvae (bloodworm), except when being tested.

5.3.2 Stream tanks and experimental procedures

Experiments were carried out in a flume system, previously described in chapter 3, consisting of a stack of three glass tanks measuring 180 x 25 x 20 cm and one glass tank measuring 120 x 25 x 20 cm, which were interconnected by plastic pipes. These tanks then drained into two 60-litre sump tanks from which water was recirculated by pumping it to the top flume tank. The water flowed through the glass tanks at approximately 0.08 $m \cdot s^{-1}$. The tanks had a 2 cm layer of gravel as a substrate and a water depth of 13 cm. Partitions placed within the

glass tanks created compartments; the partitions were opaque but had panels of fine mesh to allow a directional current through the tanks. Experiments were carried out in arenas measuring 60 x 12.5 cm, and containing three evenly-spaced feeders. These were 25 ml universal tubes with a small hole drilled near the top to allow water to circulate, and a small hole near the bottom to allow live chironomids to crawl out at random times after having been placed in the feeder. A plastic mount held each universal tube so that the exit hole for the chironomids was 5.5 cm above the substrate; the feeders each received two live chironomid larvae at 11.30 and 15.00 on each day of the experiment. The experimental apparatus was in an aquarium with ambient light and temperature levels for the time of year (late July). Water temperature was recorded daily and varied between 12.9 and 13.1 °C over the course of the experiment.

Two experimental treatments, each using three fish, were used to investigate the effects of prior residence on subsequent space use and the ability to defend a feeding territory from intruders. In treatment 1 fish could move freely between feeders immediately on release into the experimental arena. In treatment 2 the arena was partitioned into three equal-sized compartments (20 x 12.5 cm), each of which contained a feeder. A single fish was placed within each compartment allowing each fish to obtain a prior residence advantage. The partitions were removed after two days, allowing the three fish in each arena to move freely between feeders. To control for handling stress, fish from both treatments were removed from the test arenas for the length of time necessary to remove the partitions.

Fish within each group were individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Replicate groups of three size-matched fish were then randomly assigned to treatment 1 or 2 and placed in the experimental arenas. Fish were allowed to acclimate overnight and observations of fish in treatment 1 began the following day. Treatment 2 fish were unable to interact and move between areas until the additional partitions had been removed on the evening of day 2, therefore observations of these fish began on day 3 of the experiment.

On observation days the position of each fish in each experimental arena was recorded at 10.00, 11.30, 13.30 and 15.00. For those holding position at a feeding station I recorded which feeder the fish was nearest to, with feeder 1 being at the upstream end of each section and feeder 3 being at the downstream end. Fish holding position upstream of all three feeders were given a position score of 0. Observations of feeding behaviour and aggressive interactions were made over a five-minute period at 11.30 and 15.00, immediately after the feeders had been replenished. Feeding behaviour was logged by recording the number of successful feeding attempts by each fish, and from which feeder the chironomid had emerged. The initiator and recipient of all aggressive interactions were also noted.

There were eight replicates of each treatment that ran simultaneously between the 25th and 28th July 2000. Observations were maintained over this four day period for fish in treatment 1, whilst fish in treatment 2 were observed for only the last two days, the 27th and 28th July 2000.

5.3.3 Data analysis and statistical treatment

The questions of greatest interest in this study were whether fish given a prior residence advantage differed from fish added simultaneously to the whole arena in their use of the three different feeding sites, and the amount of food they obtained in each. Firstly, I calculated the percentage of time spent in each of the three sites and the feeding rate in each site for all individuals in both treatments. For those given a prior residence advantage I determined the percentage of time spent in their own site (the site in which they spent the first two days) and the mean percentage of time spent in the other two sites. An average was taken for each replicate and the replicate means were then compared using a paired samples t-test. The feeding rates of individuals, calculated as the number of food items taken per minute, in their own site as opposed to the other two sites were compared in a similar manner.

To compare site use between treatments I defined primary, secondary and tertiary sites for each individual based on the percentage of time spent in each site. The primary site was defined as the one in which the individual spent the greatest percentage of time, with the tertiary site being the site in which the least time was spent. Therefore, individuals within a replicate may or may not have had the same primary, secondary and tertiary sites. Nevertheless, the mean percentage of time spent in the primary, secondary and tertiary sites was calculated for each replicate for the purpose of comparing across treatments. Site use in the two treatments was compared on days 3 and 4 of the trial using two-way analysis of variance (ANOVA) with site (primary and secondary) and treatment (treatment 1

or 2) as the fixed factors, and percentage use as the dependent variable. However, because fish in treatment 1 were able to move freely about the whole arena for the duration of the trial, it is possible they had become more settled by days 3 and 4. Therefore, I also compared the site use of fish for the two days immediately after the whole arena had been made available (i.e. days 3 and 4 for those given a prior residence advantage and days 1 and 2 for those added simultaneously on day 1). An examination of the rate of food consumption in relation to site use and rate of aggressive interaction was conducted in a similar manner to eradicate any effects of settlement. To determine whether fish had any preference for downstream or upstream sites, the percentage of time spent in sites 1 and 3 on the last two days were compared between treatments. The percentage of times two or more fish were in the same site was also calculated for each replicate to determine whether site use was more exclusive in one treatment than the other.

The rate of aggression per minute was calculated for each individual. The average rate of aggression per replicate was then calculated and compared across treatments using an independent samples t-test. All percentage data were normalised by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for two-tailed tests of significance.

5.4 Results

Fish given a prior residence advantage did not use their 'own' original territory significantly more than the other two territories when they were free to use the

whole arena on days 3 and 4 (paired samples t-test: $t_7 = 1.23$, $P = 0.260$). On 50% of occasions the territory used most frequently by fish given a prior residence advantage on days 3 and 4 was the territory in which the fish spent the first two days. However, this did not differ significantly from what you would expect by chance (i.e. 33%; $\chi^2 = 3.06$, d.f. = 1, $P > 0.05$). Indeed, fish in both treatments had similar patterns of site use, having a favoured site in which they spent approximately 50% of their time and using a secondary site less frequently (two-way ANOVA: comparison of regression slopes, $F_{1,28} = 1.55$, $P = 0.224$; effect of site, $F_{1,28} = 78.41$, $P < 0.001$; effect of treatment, $F_{1,28} = 0.25$, $P = 0.623$; see also Fig. 5.1). There was also no significant difference between treatments in the pattern of site use when fish were first able to use the whole arena (i.e. days 3 and 4 for those given a prior residence advantage and days 1 and 2 for those added simultaneously on day 1; two-way ANOVA: comparison of regression slopes, $F_{1,28} = 0.07$, $P = 0.790$; effect of site, $F_{1,28} = 62.05$, $P < 0.001$; effect of treatment, $F_{1,28} = 0.94$, $P = 0.341$). Fish in both treatments tended to spend a greater percentage of time at the downstream end of the arena in site 3, rather than the upstream end in site 1 (two-way ANOVA: comparison of regression slopes, $F_{1,28} = 0.30$, $P = 0.590$; effect of site, $F_{1,28} = 6.52$, $P = 0.016$; effect of treatment, $F_{1,28} = 0.04$, $P = 0.851$; Fig 5.2). There was no difference between treatments in the percentage of time in which two or more fish were found together in the same site (independent samples t-test, $t_{14} = 0.69$, $P = 0.502$).

The feeding rates of fish in the two treatments did not differ when the whole arena was made available (independent samples t-test: $t_{14} = 0.18$, $P = 0.863$). Fish given a prior residence advantage were not found to feed predominantly

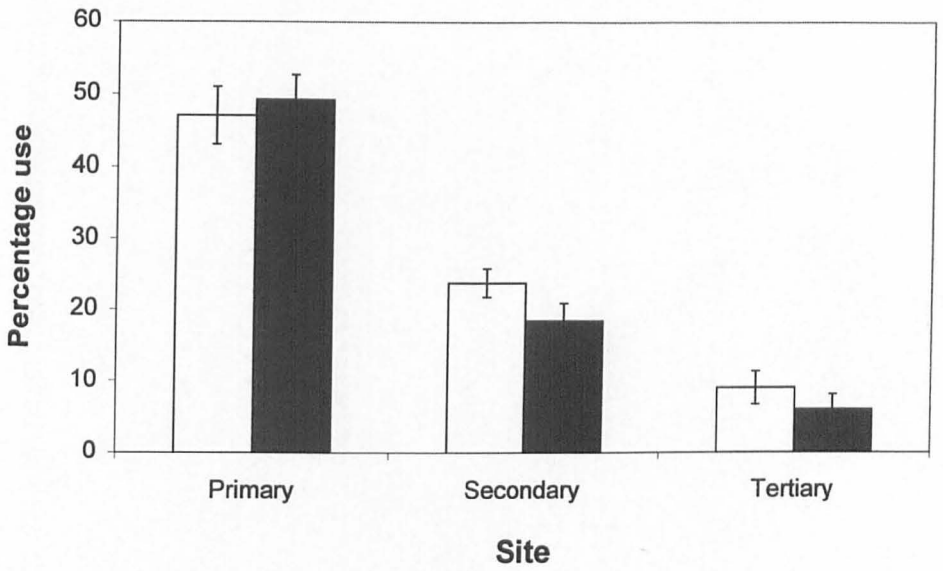

Figure 5.1. Percentage use (± SEM) of primary, secondary and tertiary sites on days 3 and 4 of the experiment for fish given a prior residence advantage (open bars) and those added simultaneously to the whole arena on day 1 (shaded bars).

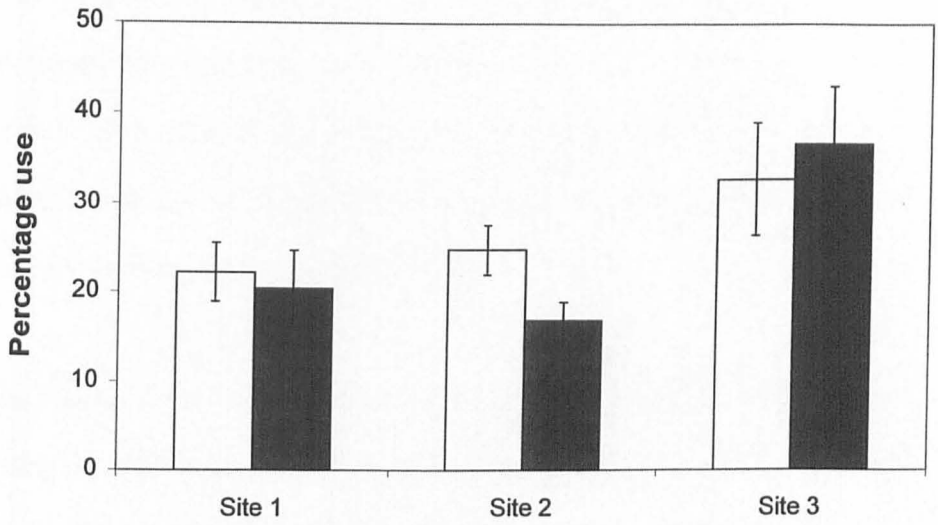

Figure 5.2. Percentage use (± SEM) of sites 1, 2 and 3 on days 3 and 4 of the experiment for fish given a prior residence advantage (open bars) and those added simultaneously to the whole arena on day 1 (shaded bars).

from the site in which they spent the first two days of the trial (paired samples t-test: $t_7 = 0.95$, $P = 0.372$). Indeed, fish from the two treatments showed similar patterns of food consumption in relation to site use (see Fig. 5.3) with more food being eaten, not surprisingly, in the primary site where a greater percentage of time was spent than in the tertiary site (two-way ANOVA: comparison of regression slopes, $F_{1,24} = 0.05$, $P = 0.826$; effect of site, $F_{1,24} = 13.17$, $P = 0.001$; effect of treatment, $F_{1,24} = 0.10$, $P = 0.757$).

There was, however, a significant difference in the rate of aggressive interactions between the two treatments, with fish that were given a prior residence advantage being more aggressive than those that were added simultaneously to the arena on day 1 (independent samples t-test: $t_{14} = 2.74$, $P = 0.016$; Fig. 5.4).

5.5 Discussion

Prior residence and its benefits have been well documented in many animals, including birds (e.g. Koivula et al. 1993; Tobias 1997), fish (e.g. Brännäs 1995; Beaugrand et al. 1996; Cutts et al. 1999a), and frogs (e.g. Wells 1978; Baugh & Forester 1994). It is perhaps surprising, therefore, that there were no significant differences in feeding behaviour and site use between individuals that had been given a prior residence advantage and those that had not, thus providing no support for my first two hypotheses. The strength of prior residence in terms of its influence on contests, however, has been shown to vary both within and between species. For example, Chellappa et al. (1999) have shown that prior residence advantage is the key factor in determining the outcome of contests

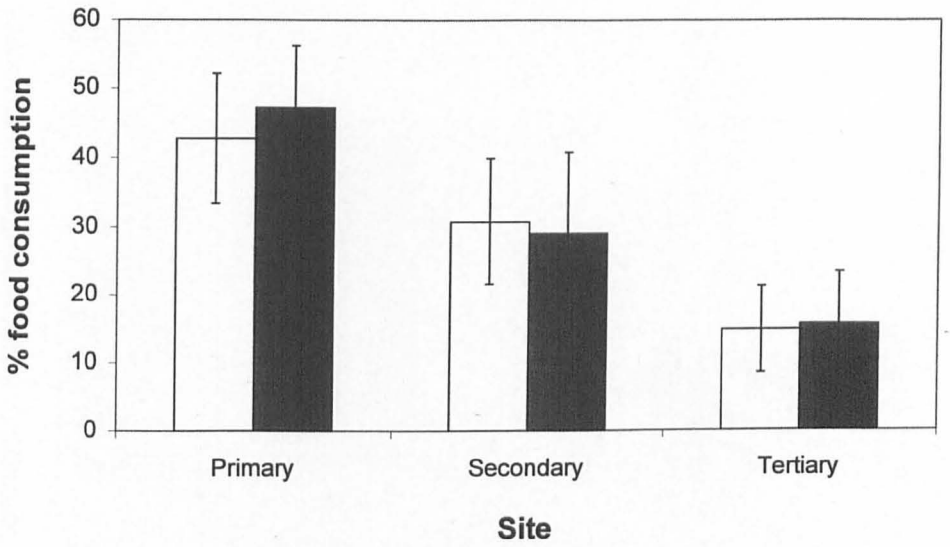

Figure 5.3. Percentage (± SEM) of food consumed in primary, secondary and tertiary sites when the whole arena had been made available, i.e. days 3 and 4 for those given a prior residence advantage (open bars) and days 1 and 2 for those added simultaneously on day 1 (shaded bars).

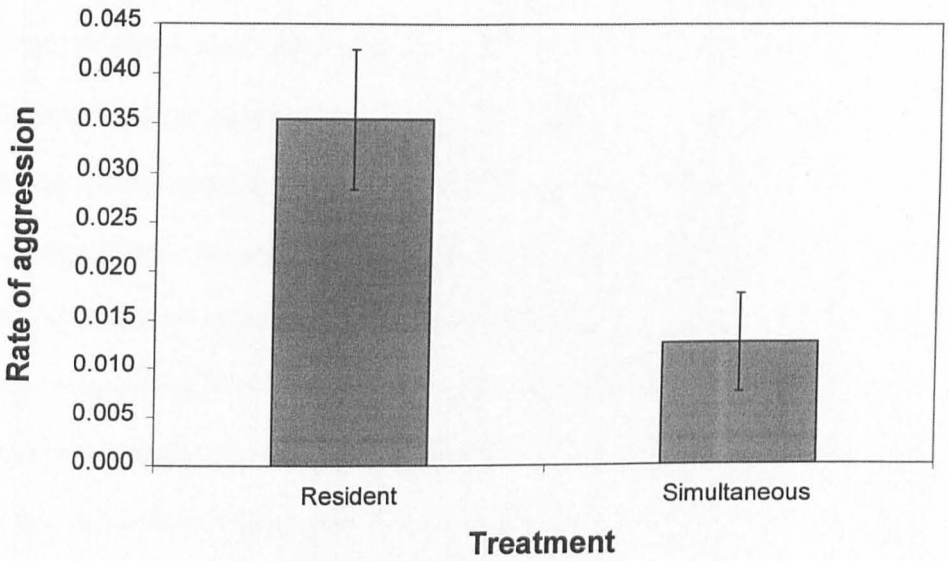

Figure 5.4. The rate of aggression (± SEM) per minute when the whole arena had been made available, i.e. days 3 and 4 for those given a prior residence advantage – resident – and days 1 and 2 for those added simultaneously on day 1 – simultaneous.

between male freshwater angelfish, irrespective of the relative size of the intruder. In contrast, although Turner (1994) found prior residence to be an important determinant of the outcome of fights between male mouth brooding cichlids its effect could be overcome by a size advantage to the intruder. This difference between species can perhaps be explained by a difference in their natural habitats, with angelfish being found in more dense vegetation than mouth brooding cichlids where assessment of relative size may be more difficult and thus less important in resolving conflict (Chellappa et al. 1999). For individuals of the same species, Rhodes & Quinn (1998) found that in aquarium experiments prior residence did not influence competitive outcome in wild coho salmon parr, but did in hatchery reared parr. This contrast between the two groups was attributed to the difference in prior experience brought about by rearing conditions.

Prior residence has previously been shown to influence various aspects relating to fitness in Atlantic salmon fry (e.g. Cutts et al. 1999a,b; O'Connor et al. 2000a; chapter 4). For example, O'Connor et al. (2000a) found that individuals introduced to semi-natural stream arenas at different times showed similar levels of site fidelity, but differed in growth rate, with those that arrived first able to grow faster than did those that arrived later. Furthermore, in chapter 4 slightly younger individuals of the same stock used in this experiment did benefit from prior residence, with those arriving first spending longer periods of time in good quality feeding sites and subsequently obtaining more food than those that arrived later. This raises the question as to why individuals in this experiment did not gain from a period of prior residence. The most obvious suggestion is

that perhaps two days was not long enough to provide an advantage. However, previous work on Atlantic salmon parr has shown that one day is sufficient to confer an advantage (see Huntingford & García de Leániz 1997). Dearborn & Wiley (1993) have shown that the advantage that resident, captive white-throated sparrows have over intruders increases with the length of the prior residence period. However, they also show that a short period of time (i.e. two days) is enough to produce an advantage. It is unlikely, therefore, that fish in this experiment did not receive the opportunity to gain a resident's advantage.

The failure of individuals to monopolise a site, despite having a resident's advantage, may result from the characteristics of each site. The availability of food at any time was unpredictable because the feeders released food at random times depending on when the bloodworm escaped. Furthermore, food items within the feeders, although not available to eat, were always visible. Therefore, rather than adopt the usual sit-and-wait approach in which passing drift items are caught from one focal point (Stradmeyer & Thorpe 1987), individuals within this experiment may have gained more food by adopting a more active search approach similar to that used by benthic feeders. Salmonids that feed on benthos have previously been shown to be non-territorial (see Nakano et al. 1999), and this may be a factor in explaining why prior residents did not feed predominantly from the site in which they spent the first two days. Grand & Grant (1994) have also shown that whilst resource defence was effective in spatially predictable environments, an active, scrambling approach was more effective in unpredictable environments. However, the same feeding system had previously been used in chapter 4 where prior residents were shown to gain an advantage in

terms of feeding rate. In contrast to chapter 4 where sites varied in quality in terms of the amount of food received, all sites in this experiment received the same amount of bloodworm per day. Therefore whilst prior residents in chapter 4 gained an advantage in using territories where more food was available, residents in this experiment may not have gained any advantage over individuals that all arrived simultaneously because sites were equal in terms of food availability. Another contributory factor may be the density of fish used. As individuals used in this experiment were slightly larger than those in chapter 4 only three fish were placed in an arena of the same size in which six were placed in the previous experiment. This may have caused competition to be less intense in both treatments thus negating any advantage in access to food that residents would have over those arriving simultaneously.

Although prior residents in chapter 4 acquired significantly more food than those arriving later, they were not territorial in the sense that they defended exclusive areas in which they fed (see Kalleberg 1958). As suggested in chapter 4, this may have been due to the nature of the feeding system whereby fish holding position near the back of the arena could acquire more food than an individual which remained faithful to one feeding site. This problem was exacerbated in this study by the lower densities and equal food availability used. One way of reducing this problem would be to ensure that fish could not see the amount of food that was available at each site.

Despite the lack of difference between the treatments in terms of site use and feeding rate, there was a difference in the rates of aggression with prior residents

being more aggressive than were those that arrived simultaneously when the whole arena was made available. This supports my third hypothesis and suggests that the period of site residence did indeed influence the fish's behaviour, making them more likely to be aggressive to other individuals competing for the same food supply. However, this increased level of aggression did not lead to the exclusion of other individuals and therefore provided no support for my fourth hypothesis. This finding suggests that the benefits of the active search method outweighed the costs of being attacked. It is worth noting that the rates of aggression witnessed in this experiment were a third of those witnessed in chapter 4, supporting the proposal that the lower densities of fish used in this experiment decreased the intensity of competition.

Previous studies have modelled the outcome of contests on the basis of fighting asymmetries and state-dependent influences, such as the level of energy reserves (e.g. Leimar & Enquist 1984; McNamara & Houston 1989). These studies suggest that animals should be more persistent and willing to take risks where the perceived value of a contested resource is high. This study supports this view because individuals were apparently unwilling to exclusively defend a resource that was unpredictable in nature. This argument has gained supportive evidence in a number of different situations. For example, Nijman & Heuts (2000) have shown that the value of the resource is important in determining the outcome of contests in fish of seven different species. They show that residents won over intruders more frequently in aquaria that provided habitat enrichment than in aquaria that did not. The resident's dominance advantage, in terms of previous occupation, was therefore expressed to a greater degree when the value of the

resource was high. In addition, Haley (1994) found that male northern elephant seals were likely to incur greater costs, by fighting for longer or against heavier males, when the reproductive payoffs were higher. It is therefore important when attempting to predict the manner in which individuals will compete to assess the value and nature of the resource.

CHAPTER 6: SYMPATRIC ASSOCIATION INFLUENCES WITHIN-SPECIES DOMINANCE RELATIONS AMONG JUVENILE ATLANTIC SALMON AND BROWN TROUT

6.1 Abstract

Size and aggressiveness are determinants of social dominance in many vertebrate species, including juvenile stream-dwelling salmonids. I used semi-natural stream channels, landscaped to provide a range of depths, to test whether the factors influencing the formation of social hierarchies are similar in single- and mixed-species groups of Atlantic salmon and brown trout. I also tested whether Atlantic salmon and brown trout have similar feeding rhythms during the day and whether dominant and subordinate individuals feed at alternative times, both under allopatric and sympatric conditions. The results show that although size appeared to be a good predictor of feeding success of both Atlantic salmon and brown trout in allopatry, when these species were in direct competition size could no longer be used to predict feeding success accurately. In contrast, rate of aggression was positively correlated with feeding success in both allopatry and sympatry. However, the timing and rate of feeding of dominants and subordinates differed significantly only in the allopatric trials, with subordinate individuals in the sympatric trials being able to adopt a non-aggressive alternative strategy and continue feeding. These results highlight the behavioural plasticity of juvenile salmonids that are able to adapt their feeding behaviour to the social environment, and suggest that the presence of another species with similar, but not identical, ecological requirements may increase the opportunity

for the expression of alternative behavioural strategies. The conclusion, therefore, is that the advantages of social dominance may to a large extent be specific to the species assemblage.

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Artificial stream at the University Field Station, Rowardennan

6.2 Introduction

Dominance hierarchies are widespread in the animal kingdom, being present within groups as diverse as the social, yet primitively organised, paper wasps to the socially complex anthropoid apes (Wilson 1975). The advantages gained by dominants are fairly uniform throughout, namely a priority of access to food, shelter and reproductive opportunities. However, the factors that determine dominance vary considerably. For example, dominance is established by the size and age of an individual within rank orders of antelopes, sheep and other ungulates (e.g. Barroso et al. 2000). By contrast, in dominance-structured groups of baboons and macaques, status can depend on the mother's rank, membership in a coalition or the length of time an individual's family has been associated with that troop (see Wilson 1975).

Numerous studies have been conducted on the dominance relationships formed within groups of salmonid fish, largely due to the implications of social suppression of feeding for the farming of salmonids (e.g. Alanärä & Brännäs 1996; for Arctic charr and rainbow trout), or their life-history strategies in the wild (e.g. Metcalfe et al. 1989; for Atlantic salmon). These studies have revealed positive relationships between the ability to monopolise a resource and aggressiveness (Adams et al. 1998; Cutts et al. 2001), metabolic rate (Metcalfe et al. 1995; Cutts et al. 2001) and size, although in some cases size has been shown to be a consequence rather than a cause of dominance (Huntingford et al. 1990; Adams et al. 1998).

Consistency in the abilities of individual fish to monopolise resources within allopatric assemblages has previously been shown across a range of temperatures (Kolok 1992; Magoulick & Wilzbach 1998; Cutts et al. 2001) and altitudes (Hayes & Chappell 1990). However, temperature may influence the competitive abilities of fish species relative to one another when coexisting in the same stream (Taniguchi et al. 1998; Taniguchi & Nakano 2000). Many studies on social dominance in fish have concentrated on hierarchies formed between members of the same species, with dominant individuals obtaining the most profitable sites in terms of food availability (Fausch 1984; Hughes 1992). Studies that have investigated competitive abilities in sympatric assemblages have shown that size and aggression are key determinants of dominance (Fausch & White 1986, Nakano 1995a), as they are in allopatric assemblages of the same species (Fausch 1984; Nakano 1995b). Here I test by direct comparison whether the factors influencing the formation of social hierarchies are similar under allopatric and sympatric conditions. I study the formation of hierarchies in Atlantic salmon and brown trout which show considerable spatial niche overlap in sympatric populations (reviewed by Heggenes et al. 1999; Armstrong et al. in press) in which trout tend to dominate salmon (Kalleberg 1958; Kennedy & Strange 1986a,b). I test the following specific predictions: 1) that size correlates positively with feeding success in both single-species (allopatric) and mixed species (sympatric) groups of Atlantic salmon and brown trout; and 2) that a similar positive correlation relates food acquisition to aggressiveness in single- and mixed-species groups.

I then examine the influence of social dominance on the feeding periodicity of fish in different social contexts. Many studies on groups of juvenile salmonids during the summer have shown that they are day-active with a peak in feeding activity at dawn and dusk, leading to the conclusion that for most of the year these fish are crepuscular feeders (e.g. Sagar & Glova 1988; Riehle & Griffith 1993; Kreivi et al. 1999). However, there is growing evidence that dominant and subordinate fish, either of the same (Alanärä et al. 2001) or different species (Alanärä & Brännäs 1997), may adopt different diel activity patterns, with subordinates feeding at a different time of day in order to avoid aggressive conflict. Therefore, I also test the following hypotheses: 3) that groups of Atlantic salmon and brown trout have the same overall diel pattern of feeding with a peak at dawn and dusk; but 4) that within this overall trend, dominants and subordinates will have different temporal patterns of feeding, both in allopatry and sympatry, in order to partition resources.

6.3 Methods

The experiment was conducted in an outdoor artificial stream (previously described in Valdimarsson et al. 1997) at the University Field Station, Rowardennan, Loch Lomondside, Scotland. The 60cm-wide stream was in the form of a continuous, approximately oval shaped loop with straight sides. Fish could be observed from within this loop since the inside walls of the channel were made from glass panels. The straight sides of the channel were each six metres in length. The variable speed impeller that pumped water around the channel occupied 2.5 m of one side. The remaining straight parts of the channel

were partitioned into three 2.25 m experimental arenas using mesh, and landscaped with fine gravel (5-25 mm diameter) to deter fish from hiding in streambed cavities. The gravel was landscaped to produce deep and shallow areas. The deep areas were situated in the middle of each arena and had curved sides with water depth at the deepest point being 25 cm. Shallow water areas (10 cm deep) were located on both sides of the deep water in each section. The surface velocity of the water varied continuously from 0.12 $m \cdot s^{-1}$ in the shallow water to 0.07 $m \cdot s^{-1}$ in the deeper water. Six large boulders were placed at regular intervals through each arena to provide fish with the option to shelter from the current. The sections between the experimental arenas were landscaped so as to produce a water depth similar to that in the shallow areas (10 cm) to decrease turbulence and smooth the flow through the channel. The outer side of the channel was marked every 15 cm along its length in order to define fifteen zones per arena (zone 1 being at the upstream end) to allow referencing of the recorded positions of the fish.

Water temperatures were approximately ambient (as there was a constant turnover of fresh water pumped from Loch Lomond into the channel) and ranged from 10.9-18.1 °C during the study. The channel was outdoors thus light levels were also ambient. The fish were provided with a steady supply of live bloodworms (chironomid larvae) through the day. The bloodworms were dispensed from small bottle caps filled with water placed on a 24hr belt feeder. In this way a bottle cap would fall from the belt feeder approximately every two hours dropping the bloodworms onto a fine net mesh partly submerged in the water. The bloodworms then crawled through this fine mesh and became

available for the fish to eat. Fish were prevented from feeding on the bloodworms whilst on the fine mesh by a surrounding coarse metal mesh. Fish were provided with 2% of their total body weight in food per day. This bloodworm supply was supplemented by a low level of zooplankton in the water pumped from Loch Lomond.

To examine the formation of social hierarchies and diel behavioural rhythms of salmon and trout, and to determine whether there was any difference between the two species, two single-species (allopatric) experimental treatments were used, in which either six salmon or six trout were placed in separate experimental arenas. Additionally, in order to determine whether inter-specific competition affects the formation of a social hierarchy or the behavioural patterns of either species, a third experimental treatment was conducted in which three salmon and three trout were placed in an experimental arena together (sympatric treatment). Fish in all three treatments were approximately size-matched for two main reasons. Firstly, to reduce any confounding effects of large size differences (size differential > 20%), as my primary objective was to investigate species and assemblage differences. Secondly, to ensure that I was investigating competition for microhabitats used commonly by both species. There is considerable niche segregation of different age-classes in both species (Kennedy & Strange 1982; Heggenes et al. 1999) and therefore fish of widely different size might not compete. Replicates of the three treatments were run simultaneously in different arenas of the stream channel to prevent any confounding effects of temperature or time of year influencing the results.

The fish used were wild-caught salmon (fork length: mean ± SE = 68.4 ± 0.62 mm; weight = 3.23 ± 0.09 g) and trout (fork length = 71.1 ± 0.69 mm; weight = 3.69 ± 0.12 g) from the River Endrick, which flows into Loch Lomond. Fish were housed in two species-specific holding tanks prior to experimentation and were caught less than one week before experiments began. Fish were individually marked on their dorsal and caudal fins using small injections of alcian blue dye, after anaesthetisation using benzocaine. Fish were marked in the evening and then placed individually in separate 0.5 l opaque plastic containers at the back of the experimental arena in which they were to be observed. The open top was covered with mesh to prevent the fish from escaping and a rock was placed in each one to weigh it down. The containers were placed facing the direction of flow with several holes drilled into each to allow water to flow through. This procedure allowed the fish to recover from the effects of anaesthesia without being able to sample their new surroundings. The mesh was removed from each container the following morning, allowing the fish to enter the main part of the arena simultaneously.

The observations on each group of fish were continued over the five days following release. Each day was split into eight 3-hour periods and the fish observed for 3-5 of these periods per day. During each selected three-hour period the fish were observed twice, with an hour separating the observation periods. During each observation period each fish was individually identified and its position in terms of zone noted. In addition, the vertical position of the fish (either resting on the bottom or swimming in the water column) and whether the fish was sheltering adjacent to a boulder were also recorded. The fish was

then watched for one minute during which feeding attempts were counted and the aggressive interactions initiated and received were recorded, along with the identity of the other fish involved in each bout. The aggression witnessed varied from displays to charges and nips (see Keenleyside & Yamamoto 1962 for more details of aggressive interactions in young salmonids).

Light intensity was measured during each observation period using a photometer (Skye Instruments SKL 300, range 0.01-2000 lx) and recorded as the mean of two measurements made just above the water surface, in the middle of the straight section on either side of the channel. Water temperature was measured using a digital thermometer placed permanently in the stream.

After the data had been collected on each group, the fish were removed and a different group of fish was placed in the test arena. In total, the sympatry and salmon in allopatry treatments were replicated 8 times and the trout in allopatry treatment was replicated 6 times, with new fish in each trial. The experiments were carried out between 30th August and 15th October 1999.

6.3.1 Ethical note

All experimental procedures, including anaesthetisation and marking, were carried out under U.K. Home Office Licence. Fish were kept at densities similar to those that would be experienced in the wild (see Grant & Kramer 1990), and were monitored closely to ensure that fish could be removed if contests escalated to a point where injury could occur. However, this was only required on one

occasion when one individual sustained a degree of fin damage. The fish was removed and returned to the holding tank where it subsequently recovered, and was returned to the wild along with all other experimental fish at the end of the trials.

6.3.2 Data analysis

For the purpose of data analysis, the eight three-hour periods during which observations were made were combined to give the following periods: morning (0600-1200 hours), afternoon (1200-1500 hours), evening (1500-2100 hours) and night (2100-0600 hours). The data were split into the following categories for comparison: salmon in allopatry, trout in allopatry, salmon in sympatry (with trout) and trout in sympatry (with salmon). In order to evaluate the effect of body size on behaviour while standardising for size differences between trials, the relative body length of each fish was calculated as its body length as a proportion of that of the largest in its group of six fish. To determine the influence of relative size on behaviour whilst comparing fish in different treatments I performed analyses of covariance (ANCOVA) with relative length as the covariate, category of fish as the fixed factor and individual feeding rate and aggression initiated as the dependent variables. I also used analysis of covariance to determine whether feeding rate (dependent factor) could be predicted from the rate of aggression initiated (log x +1 transformed). As the above analysis compared behaviour within replicates it is possible that pseudo-replication may affect the results, in that the behaviour of one individual may have influenced the behaviour of others. To alleviate any fears that conclusions

drawn from these analyses were over-optimistic I conducted analysis of covariance tests with tank included as a variable. In none of these tests was tank revealed to be a significant explanatory factor and my conclusions can therefore be considered valid.

To test for patterns in feeding rates over a 24-hour period and over the course of the experiment, the four categories of fish were further split on the basis of social status, with two dominants being defined in each replicate group as the two most aggressive fish over the five days of observation. Their feeding rate, during each time period or on each day, was then averaged to give a single mean score for the dominants of that particular replicate group. In sympatric trials where the two dominant fish were a salmon and a trout, an average was not taken in order to maintain the integrity of the species data. In these cases, values were obtained for dominant salmon in sympatry and dominant trout in sympatry. Mean scores for the remaining subordinate fish of each species in each replicate were calculated in a similar manner. Repeated measures analysis of variance (ANOVA) was then carried out on feeding rate with either time period or day of experiment as the within-subject factor, and treatment (allopatry and sympatry), species (salmon and trout) and social status (dominant and subordinate) as the between-subject factors. Repeated measures ANOVAs were also carried out on the two allopatric treatments alone in order to determine species differences in behaviour without treatment as a confounding variable.

The percentage of time spent in deeper water was calculated for each individual by determining the number of times that the fish occurred in zones 6-10 (deeper

area), as opposed to zones 1-5 and zones 11-15 (shallow areas), and calculating this as a percentage of the overall number of observations. The percentage of time spent touching the substrate, as opposed to swimming in the water column, was also calculated for each individual. Replicate means were then calculated for these behavioural variables in the manner described above. I used analysis of covariance to determine the influence of species, treatment and social status (fixed factors) on the percentage of time in deep water and the percentage of time spent on the substrate (dependent factors).

To test for patterns of aggression over a 24-hour period and over the course of the experiment, separate analyses were conducted that took account of the varying levels of opportunity to attack different categories of fish. For example, individual salmon in allopatry and trout in allopatry had the same level of opportunity to attack other individuals of their own species, and these two levels of aggression could therefore be directly compared. In contrast, a salmon in sympatry with trout had the opportunity to attack three trout but only two other salmon. For this reason, aggression in sympatry was analysed by comparing levels of salmon – salmon aggression with trout – trout aggression, and salmon – trout aggression with trout – salmon aggression. The replicate mean for each category of fish was found and then analysed using repeated measures ANOVA to test for patterns of aggression through the day and over the course of the experiment. Social status was not included in the analysis of aggression data as status was itself defined by the level of aggression. Chi-squared analysis was performed to compare the numbers of displays, chases, charges and nips used in each treatment by each species, to test for possible variation in the nature of

aggression used under different environmental conditions. All percentage data were normalised by arcsine transformation prior to use in parametric tests, and all quoted probabilities are for two-tailed tests of significance.

6.4 Results

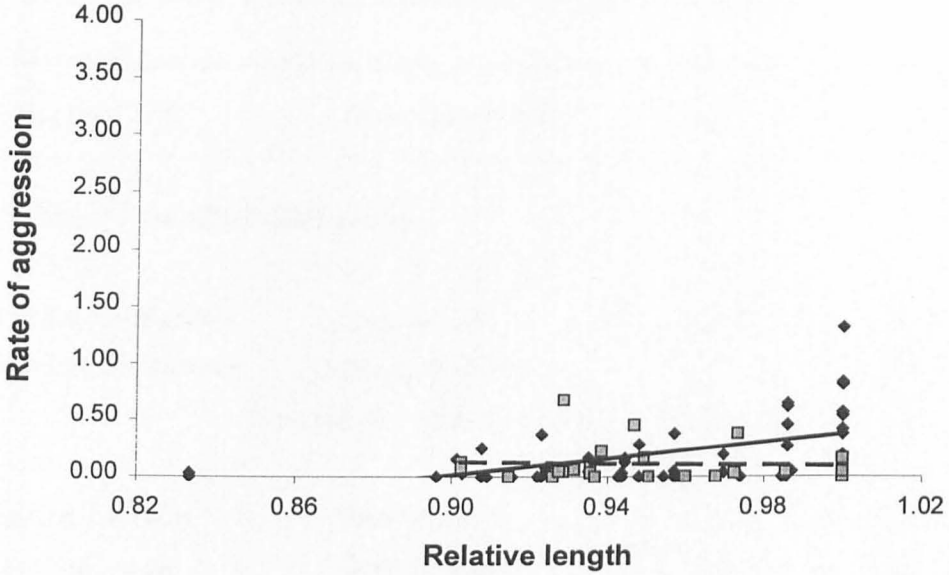
6.4.1 Aggression

Comparison of the relationship between relative length and the rate of aggression initiated for salmon in allopatry versus salmon in sympatry reveals that there was a significant difference between the categories of fish, with the largest salmon in allopatry being the most aggressive fish, whilst this was not the case for salmon in the presence of trout (Table 6.1; Fig. 6.1a). The same pattern was witnessed when comparing trout in allopatry with trout in sympatry (Table 6.1; Fig. 6.1b). There was also a significant difference between the species in the rate of aggression that they initiated when in sympatry, with trout being significantly more likely to be defined as dominants than salmon ($\chi^2 = 6.25$, d.f. = 1, P = 0.012). In addition, when testing for time of day effects there was a significant effect of fish category in each of the three inter-specific comparisons: salmon in allopatry versus trout in allopatry, salmon – trout versus trout – salmon, and salmon – salmon versus trout – trout, with trout initiating more aggression than salmon in each case (Table 6.2). A comparison of the percentage of times salmon attacked salmon and trout attacked trout in sympatry revealed that salmon directed a greater percentage of aggression to members of their own species than trout did (independent samples t-test: $t_{22.5} = 2.20$, P = 0.038). These

Table 6.1. Summary of results from a series of analyses of covariance to determine the influence of relative size and treatment on level of aggression initiated and feeding rate.

Source of variation	d.f.	F	P
Level of aggression initiated			
Salmon in allopatry vs. salmon in sympatry			
Comparison of regression slopes	1,67	4.58	0.036
Trout in allopatry vs. trout in sympatry			
Comparison of regression slopes	1,54	6.00	0.018
Feeding rate			
Salmon in allopatry vs. salmon in sympatry			
Comparison of regression slopes	1,67	1.27	0.263
Effect of relative length	1,68	3.17	0.079
Effect of category of fish	1,68	0.55	0.463
Trout in allopatry vs. trout in sympatry			
Comparison of regression slopes	1,54	1.33	0.255
Effect of relative length	1,55	2.06	0.157
Effect of category of fish	1,55	3.25	0.077

a)



b)

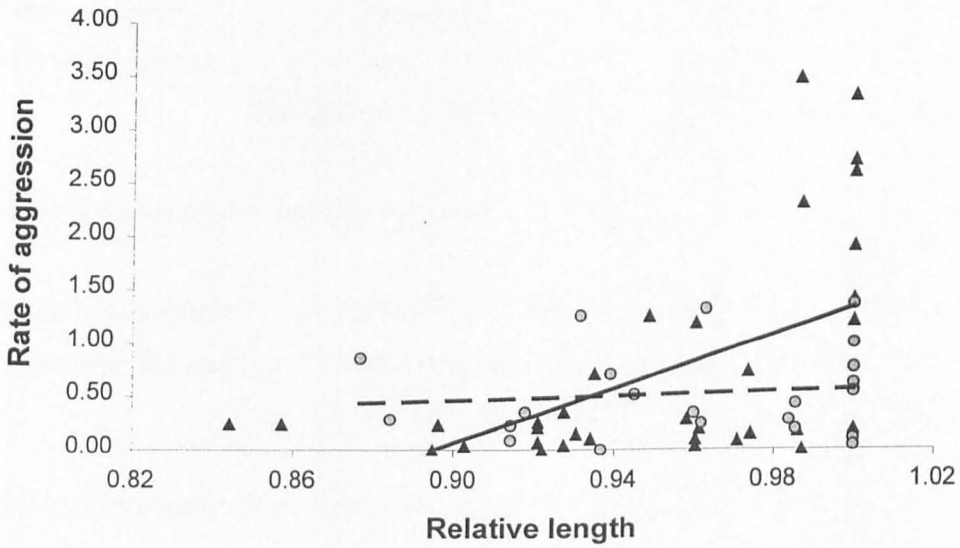


Figure 6.1. The rate of aggression initiated per minute by individual fish against their length for a) salmon in allopatry (filled diamonds; solid line) and salmon in sympatry (shaded squares; dashed line) and b) trout in allopatry (filled triangles; solid line) and trout in sympatry (shaded circles; dashed line). Length is expressed relative to the largest fish in the group (= 1.0).

Table 6.2. Summary of results from repeated measures ANOVAs for the effect of time period and day of experiment on the level of aggression initiated.

Category of fish	Source of variation	df	F	P
Within-subject effect: time period				
Salmon in allopatry	Time period	2,24	1.23	0.311
vs. trout in allopatry	Category of fish	1,12	43.55	< 0.001
	Time period * category of fish	2,24	0.39	0.682
Salmon – salmon	Time period	2,28	2.54	0.097
vs. trout – trout	Category of fish	1,14	4.73	0.047
	Time period * category of fish	2,28	0.37	0.691
Salmon – trout	Time period	2,13	0.46	0.643
vs. trout – salmon	Category of fish	1,14	8.44	0.012
	Time period * category of fish	2,13	0.64	0.544
Within-subject effect: day of experiment				
Salmon in allopatry	Day of experiment	4,7	2.34	0.154
vs. trout in allopatry	Category of fish	1,10	30.88	< 0.001
	Day * category of fish	4,7	2.97	0.099
Salmon – salmon	Day of experiment	4,9	5.44	0.017
vs. trout – trout	Category of fish	1,12	1.74	0.211
	Day * category of fish	4,9	7.70	0.006
Salmon – trout	Day of experiment	4,9	0.89	0.507
vs. trout – salmon	Category of fish	1,12	10.57	0.007
	Day * category of fish	4,9	1.99	0.179

results confirm that trout were generally more aggressive and tended to dominate salmon.

There was no significant time of day effect in the amount of aggression initiated for any category of aggression (Table 6.2). There was also no consistent decline in aggression over the 5-day course of the experiment, with the significant day effect for salmon – salmon and trout – trout aggression representing a decreased level of aggression on day 2 in relation to days 1, 3, 4 and 5 (cubic term of polynomial contrasts: $F_{1,12} = 8.27$, $P = 0.014$).

There were significant differences in the nature of aggression used both between species and between treatments. For fish in allopatry, salmon were more likely to use charges than were trout, with correspondingly fewer displays and chases ($\chi^2 = 31.21$, d.f. = 3, $P < 0.001$). When comparing both species in allopatry and sympatry there were significantly more displays, and fewer charges and nips, than would be expected in sympatry ($\chi^2 = 32.47$, d.f. = 3, $P < 0.001$; see Fig. 6.2). There was also a significant difference in the aggression used by salmon and trout against their own species in sympatry. As in allopatry, salmon attacking salmon were less likely to display or chase and more likely to charge than were trout attacking trout ($\chi^2 = 14.76$, d.f. = 3, $P = 0.002$). However, there was no significant difference between the type of aggression used by salmon to attack trout, and trout to attack salmon ($\chi^2 = 3.86$, d.f. = 3, $P = 0.277$).

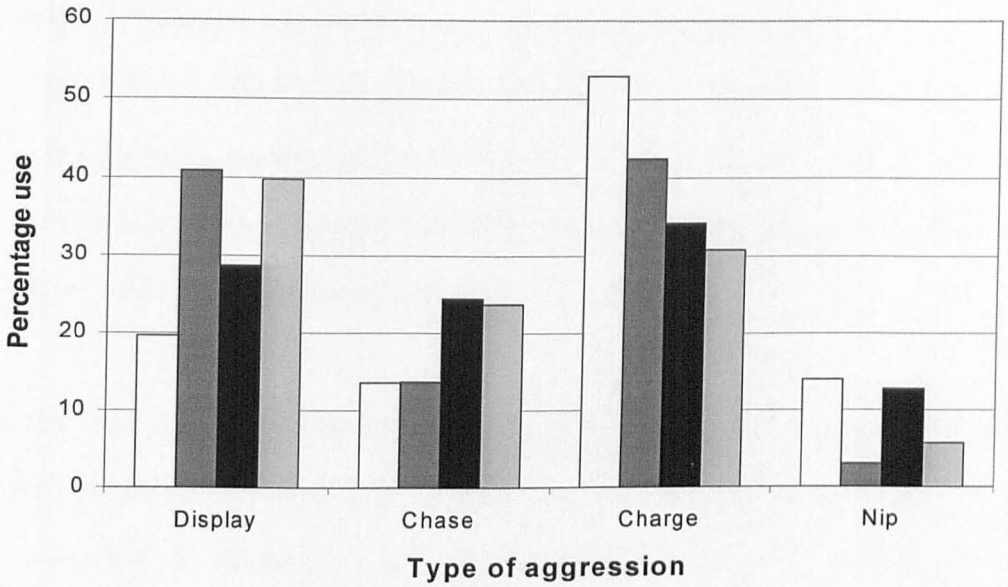


Figure 6.2. Percentage use of displays, chases, charges and nips by salmon in allopatry (open bars), salmon in sympatry (dark grey bars), trout in allopatry (filled bars) and trout in sympatry (light grey bars).

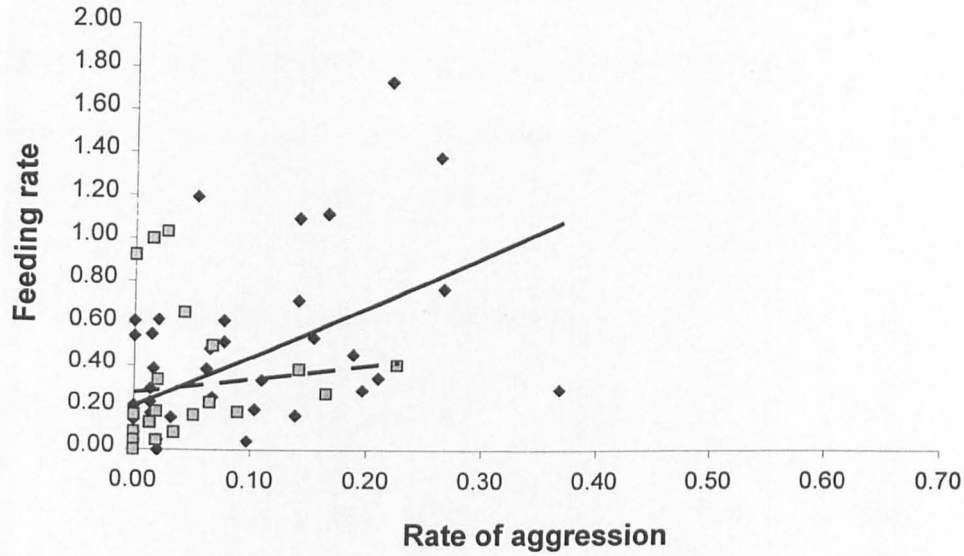
6.4.2 Feeding

There was a trend for larger fish to feed at a higher rate than smaller fish in both salmon in allopatry ($r^2 = 0.081$, $F_{1,45} = 3.96$, $P = 0.053$) and trout in allopatry ($r^2 = 0.128$, $F_{1,34} = 5.00$, $P = 0.032$). However, when comparing salmon in allopatry with salmon in sympatry, and trout in allopatry with trout in sympatry, there was no significant effect of length on feeding rate, and no significant difference in the slopes of the regression lines (Table 6.1).

There was a positive relationship between the rate of aggression initiated and feeding rate for both salmon in allopatry and salmon in sympatry (ANCOVA: comparison of regression slopes, $F_{1,67} = 1.69$, $P = 0.198$; comparison of regression elevations, $F_{1,68} = 0.03$, $P = 0.860$), with more aggressive fish gaining significantly more food than less aggressive fish (effect of rate of aggression, $F_{1,68} = 17.36$, $P < 0.001$; Fig. 6.3a). There was a similar relationship for trout in allopatry and trout in sympatry (ANCOVA: comparison of regression slopes, $F_{1,54} < 0.01$, $P = 0.999$; effect of rate of aggression, $F_{1,55} = 11.34$, $P = 0.001$). Trout in sympatry also gained significantly more food than trout in allopatry for an equivalent amount of aggression (comparison of regression elevations, $F_{1,55} = 4.99$, $P = 0.030$; Fig. 6.3b).

There was no significant variation in feeding rate through the day for any category of fish (Table 6.3). There was a significant status effect, with dominant fish feeding at a higher rate than subordinates. However, a significant interaction between treatment and status indicates that the effect of status was not the same

a)



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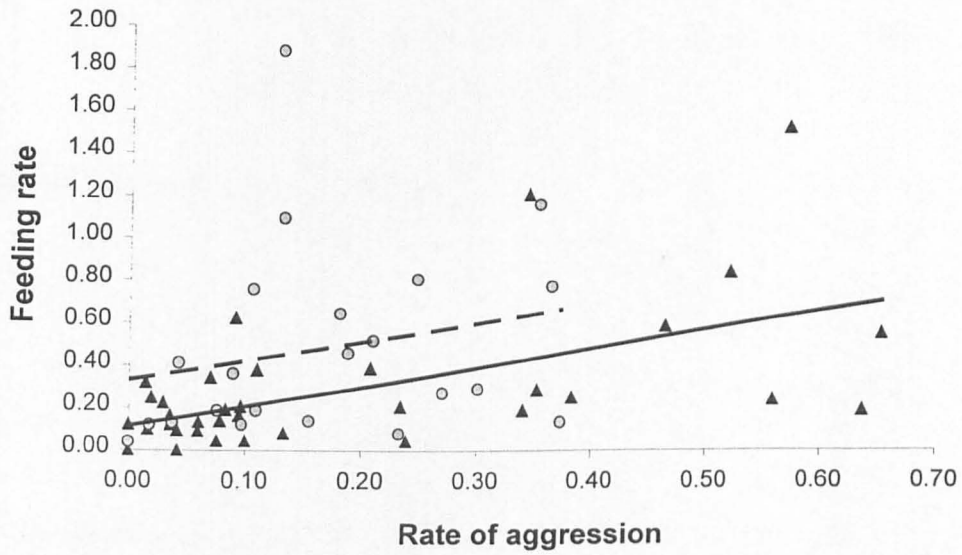


Figure 6.3. Feeding rates (items attacked min^{-1}) of individual fish plotted against their rate of initiated aggression per minute (log x + 1 transformed) for a) salmon in allopatry (filled diamonds; solid line) and sympatry (shaded squares; dashed line) and b) trout in allopatry (filled triangles; solid line) and sympatry (shaded circles; dashed line).

Table 6.3. Summary of results from repeated measures ANOVAs for the effect of time of day on feeding rate with a) treatment included as a between-subject factor and b) treatment excluded, thus comparing only the two allopatric trials.

Category of fish	Source of variation	df	F	P
a) Treatment included as between-subject factor				
Within-subject effects	Time	2,46	0.93	0.404
	Time * treatment	2,46	0.87	0.424
	Time * species	2,46	0.11	0.896
	Time * status	2,46	0.08	0.922
	Time * treatment * species	2,46	0.63	0.539
	Time * treatment * status	2,46	0.96	0.390
	Time * species * status	2,46	2.67	0.080
	Time * treatment * species * status	2,46	0.13	0.883
Between-subject effects	Treatment	1,47	0.30	0.588
	Species	1,47	0.14	0.715
	Status	1,47	4.81	0.033
	Treatment * species	1,47	1.63	0.209
	Treatment * status	1,47	4.11	0.048
	Species * status	1,47	0.46	0.500
	Treatment * species * status	1,47	0.12	0.732

Table 6.3. continued

Category of fish	Source of variation	df	F	P
b) Treatment excluded as between-subject factor				
Within-subject effects	Time	2,23	1.98	0.160
	Time * species	2,23	0.31	0.733
	Time * status	2,23	0.78	0.470
	Time * species * status	2,23	7.41	0.003
Between-subject effects	Species	1,24	0.72	0.404
	Status	1,24	15.63	0.001
	Species * status	1,24	0.10	0.756

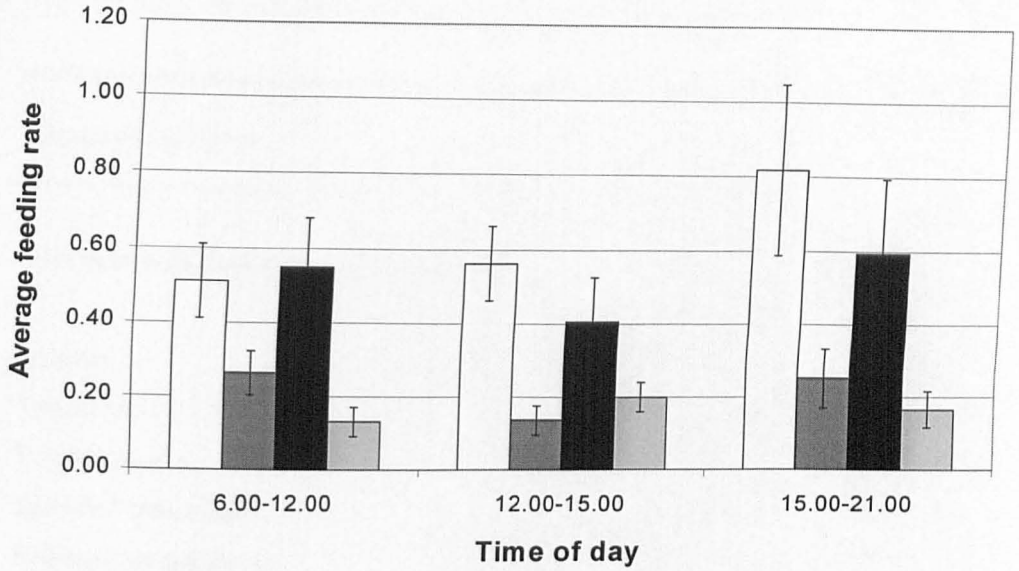
in all treatments, with there being a negligible effect of status in the sympatric treatment whilst in allopatry there was a large difference in feeding rates of fish of different status (see Fig. 6.4a & b).

When the analysis was repeated using the data from just the two allopatric trials there was no significant effect of time of day on feeding rates for either salmon or trout (Table 6.3). However, there was a highly significant status effect with dominant fish feeding at a higher rate than subordinates. There was also a significant time by species by status effect, indicating that the effect of status on diel pattern of feeding was different for the two species. This difference lay in the fact that subordinate trout ate more when dominant trout reduced their feeding rate, whilst the relationship between the feeding patterns of dominant and subordinate salmon was less clear (see Fig. 6.4a). There was no significant temporal pattern in the level of feeding when comparing across the five days of each experiment.

6.4.3 Habitat use

There were significant species and status effects on both the percentage of time spent in deeper water and the percentage of time spent on the substrate. Trout spent significantly more time in deeper water than salmon, but less time touching the substrate. Similarly, dominant fish of both species spent a greater percentage of their time in deeper water than subordinates, but significantly less time holding position on the substrate (Table 6.4; Fig. 6.5a & b).

a)



b)

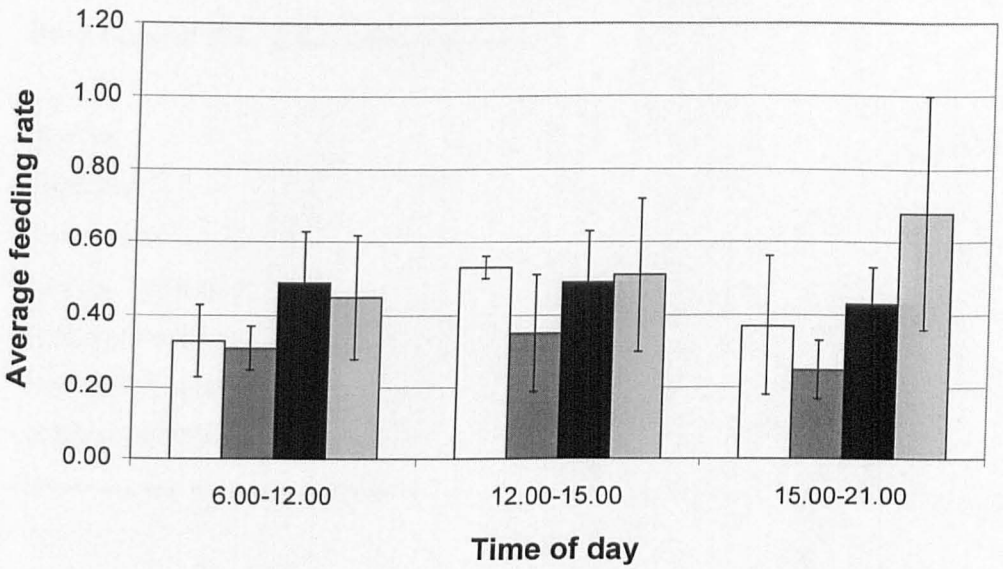
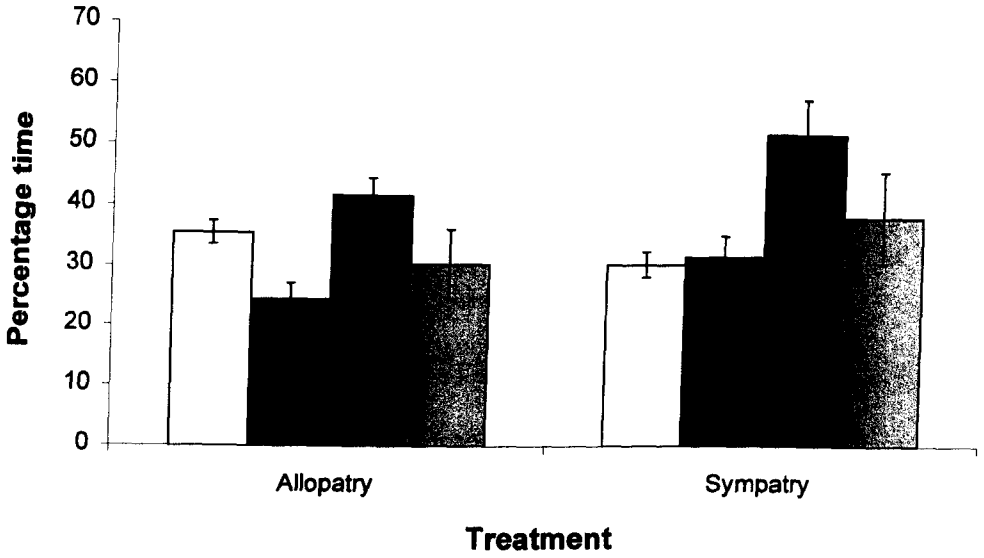


Figure 6.4. Average feeding rate (items attacked min^{-1} ± SEM) through the day for dominant salmon (open bars), subordinate salmon (dark grey bars), dominant trout (filled bars) and subordinate trout (light grey bars) in a) allopatry and b) sympatry.

Table 6.4. Summary of analyses of covariance to determine the influence of species, treatment and social status (fixed factors) on the percentage of time spent in deep water and on the substrate (dependent factors).

Source of variation	d.f.	F	P
Percentage of time spent in deep water			
Species	1,47	7.53	0.009
Treatment	1,47	1.96	0.168
Social status	1,47	5.93	0.019
Species * treatment	1,47	1.15	0.290
Species * social status	1,47	1.02	0.318
Treatment * social status	1,47	0.43	0.515
Species * treatment * social status	1,47	0.98	0.328
Percentage of time spent on the substrate			
Species	1,47	8.25	0.006
Treatment	1,47	0.94	0.336
Social status	1,47	8.02	0.007
Species * treatment	1,47	0.57	0.453
Species * social status	1,47	0.57	0.453
Treatment * social status	1,47	0.04	0.851
Species * treatment * social status	1,47	0.06	0.816

a)



b)

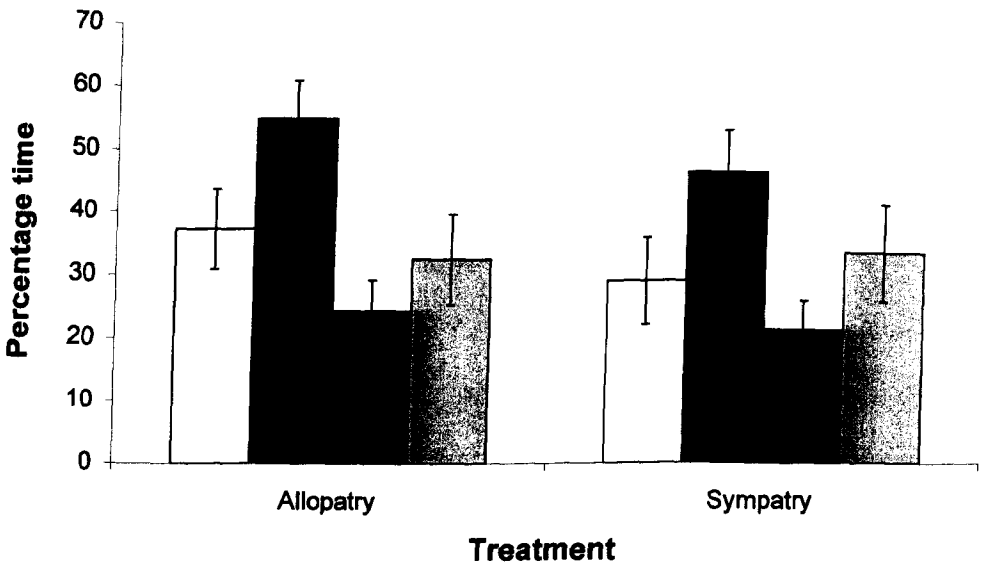


Figure 6.5. Habitat use by dominant salmon (open bars), subordinate salmon (dark grey bars), dominant trout (solid bars) and subordinate trout (light grey bars) in terms of a) percentage time spent in deep water and b) percentage time on substrate.

6.5 Discussion

Although there is a trend for larger salmon and trout to feed at a higher rate than smaller individuals in allopatry, this is not evident when comparing the behaviour of fish between treatments. These results, therefore, provide no support for my first hypothesis that food acquisition correlates positively with size in single- and mixed-species groups of Atlantic salmon and brown trout. Furthermore, my results enlarge the growing sample of contrasting results obtained when examining the relationship between size and dominance in terms of feeding success, for if I had only been interested in single-species groups I would have assumed a significant correlation between size and dominance. Such a positive correlation has previously been witnessed under a range of conditions (Jenkins 1969; Abbott et al. 1985; Nakano 1995a,b), whilst other studies have found no relationship between food acquisition and body size (Metcalfe & Thorpe 1992; Adams & Huntingford 1996). The conclusion that size is a consequence rather than a cause of dominance, with dominant fish becoming large rather than vice versa (Huntingford et al. 1990) may go some way to explaining my results. This is because large fish in sympatry did not acquire more food than smaller fish, but may have been dominant in past social experiences and thus attained large size. This argument relies on the assumption that fish can adopt different behavioural strategies that promote success in different competitive environments (see Adams & Huntingford 1996; Pettersson et al. 1996).

The positive correlation between rate of aggression and food intake has been documented before (Grant 1990; Adams et al. 1998; Cutts et al. 2001), and in the present study was present in both species in allopatry and when the two species coexisted. These results therefore provide support for my second hypothesis that aggressiveness and feed intake are positively correlated in single- and mixed-species groups of Atlantic salmon and brown trout. However, although there was a clear positive relationship between size and aggressiveness for both salmon and trout in allopatry (see also Elliott 1990; Nakano 1995b), this was not the case in sympatry. This raises the question: why were the largest fish in sympatry not the most aggressive, especially when the most aggressive fish obtained the most food? This may relate to the different competitive abilities of Atlantic salmon and brown trout. Trout are known to be more aggressive than salmon of a similar size (Kalleberg 1958; this study), and this dominance has previously been shown to affect both the spatial (Kennedy & Strange 1986b) and temporal (chapter 2) resource use of salmon in sympatry with trout. Given the presence of the competitively inferior salmon, large trout in sympatry may not need to engage in high levels of aggression. This is supported by the fact that trout in sympatry did not need to expend as much aggression to acquire a given amount of food than did trout in allopatry. Salmonids have previously been shown to adjust their methods of resource acquisition based on their relative costs and benefits. For example, brook charr (McNicol & Noakes 1981) and Arctic charr (Adams et al. 1995) have been shown to reduce their rate of aggression when current velocity increases, because the cost of defending their territory outweighs the benefit gained in terms of food acquisition.

The largest salmon in allopatry may have similarly reduced their level of aggression because in the presence of competitively superior trout they were unable to monopolise the resource in the same manner as when only smaller salmon are present. They were therefore forced to adopt alternative strategies to acquire sufficient resources. In this instance, salmon were perhaps able to obtain more food by initiating very little aggression and holding position on the substrate within deeper water, than they were by being aggressive. The non-aggressive individuals may have been able to remain vigilant and capture any food that aggressive trout higher in the water column missed whilst concentrating on fighting. In contrast, salmon that were aggressive in sympatry were the only category of fish that spent less time in deep water in sympatry than in allopatry, presumably because they were displaced by competitively superior trout. A similar non-aggressive strategy has been witnessed in groups of Atlantic salmon (Adams et al. 1998) and rainbow trout (Pettersson et al. 1996), thus supporting the proposal that minimising energy expenditure, through low levels of aggression and attempts at feeding, at the expense of maximising food intake may be the optimum strategy for subordinates (Metcalfe 1986). In support of this argument, Elliott (1990) found high levels of aggression to be extremely costly in terms of feeding. Similarly, Cutts et al. (2001) found no relationship between competitive ability and subsequent growth because dominants only achieved a greater energy intake through greater energy expenditure on increased aggression and feeding attempts. A similar switch to an alternative feeding strategy under different environmental conditions has previously been witnessed in competition between Dolly Varden and white-spotted charr in Japanese streams. In this instance, a drop in the abundance of drifting prey caused the

competitively inferior Dolly Varden to shift to non-territorial benthic foraging whereas white-spotted charr continued to feed on the drift, thus allowing both species to coexist even when their preferred prey was limited (Nakano et al. 1999). Another possible explanation for the change in behaviour of large fish in sympatry is that they were more familiar with conspecifics, having been kept in species-specific holding tanks, and therefore spent longer assessing the fighting ability of unfamiliar heterospecifics before engaging in aggression. However, this is unlikely to be the case as holding tanks initially held 70 fish of each species and trials began less than one week after fish were caught. Furthermore, evidence from previous studies suggests that aggression would be higher among unfamiliar fish (Johnsson 1997; O'Connor et al. 2000b).

I found no significant difference in the feeding periodicity of Atlantic salmon and brown trout, although there was no peak in feeding at dawn and dusk, thus providing only partial support for my third hypothesis. A lack of significant diel variation in feeding rates has previously been witnessed in wild populations of brook charr (Forrester et al. 1994). However, the overwhelming impression from studies of feeding behaviour of wild salmonids is that there is a great deal of variation in the timing of feeding between populations and species. For example, Angradi & Griffith (1990) found rainbow trout to feed throughout the day, whereas Elliott (1973) found a distinct peak at dusk for the same species in a different river. This variation is likely to stem from behavioural plasticity similar to that discussed above allowing an opportunistic switch in feeding times or feeding method, dependent on environmental conditions.

There was also only partial support for my fourth hypothesis, because whilst there was a significant difference in the feeding rates of dominant and subordinates of both species in allopatry, there was no similar discrepancy under sympatric conditions. This result may be related to the differences in behaviour between the two species, both in terms of the nature of aggression used in inter- rather than intra-specific competition, and in terms of their microhabitat choices. When comparing the nature of aggressive interactions in sympatry with those in allopatry there were significantly more displays, and correspondingly fewer charges and nips than would be expected in sympatry. The less overt aggression used under sympatric conditions may have allowed subordinates to feed at a higher rate than under allopatric conditions, as the risk of injury may select against some strategies of food acquisition (Adams et al. 1998). Sabo & Pauley (1997) have previously witnessed similar variability in the use of aggression by different populations of fish. They found that in paired size-matched competition between cutthroat trout and coho salmon, cutthroat that had previously been isolated from coho used chases, whereas cutthroat that naturally coexisted with coho used displays. The use of less overt aggression in sympatry, and the subsequent response in behaviour, may in part be explained by changing the density of conspecifics. However, this is an inevitable consequence of comparing sympatry and allopatry whilst maintaining overall biomass (see Fausch 1998) and would not be predicted to alter the rules determining who becomes dominant within species. The effect that aggression can have on the pattern of feeding was also witnessed when comparing the feeding of dominant and subordinate trout in allopatry with that of dominant and subordinate salmon in allopatry. This comparison showed that although subordinate trout ate more

when dominants reduced their feeding rate, the relationship between the feeding patterns of dominant and subordinate salmon was not as clear. This suggests that the feeding of subordinate trout was repressed to a greater extent than that of subordinate salmon due to increased levels of aggression used by dominant trout. This finding supports that of Alanärä et al. (2001), who suggest that the degree of temporal segregation in feeding will vary with the intensity of competition, with a higher degree of segregation when competition is high.

Another factor that may explain why there was little difference in feeding rates of dominants and subordinates in sympatry was the different microhabitat use of salmon and trout, with salmon spending significantly more time on the substrate than trout did. This partitioning of the habitat has previously been found both in simulated natural streams (chapter 2) and in the wild (Bremset & Berg 1999). In chapter 2 I found that the use of the substrate by salmon allowed them to occupy preferred deep-water habitats in winter alongside brown trout. However, dominant salmon using the preferred spatial niche were forced to feed at less preferred times during the day, rather than at night, in order to obtain enough food. This was due to the fact that the alternative strategy witnessed in this study would not be effective because prey are more difficult to see at night, and trout would be defending smaller territories (Valdimarsson & Metcalfe 2001) and thus would be less likely to be distracted by fighting.

6.5.1 Implications

This study highlights a behavioural plasticity in feeding behaviour that allowed subordinates to obtain enough food in spite of the presence of more dominant individuals, whether of the same or a different species. Strategies to avoid aggressive interactions include shifting the timing of feeding to avoid dominant individuals (Alanärä & Brännäs 1997; Alanärä et al. 2001) or shifting to a different foraging mode, such as benthic foraging (Fausch et al. 1997; Nakano et al. 1999) or a vigilant non-aggressive foraging strategy (Pettersson et al. 1996; Adams et al. 1998; this study). Alternative feeding strategies such as these are likely to be widespread in animal communities (e.g. Partridge & Green 1987), especially where social hierarchies prevail. This study provides evidence that the presence of a species sharing similar, but not identical, ecological preferences can create the opportunity for these alternative behavioural strategies to be expressed in a similar manner as predation risk can (Reinhardt 1999). This study therefore provides the first evidence that the structure of dominance hierarchies can be dependent on the species assemblage, as well as temperature and habitat (Dunson & Travis 1991; Fausch 1998).

CHAPTER 7: DOES DOMINANCE STATUS CORRELATE WITH GROWTH IN WILD STREAM-DWELLING ATLANTIC SALMON?

7.1 Abstract

Social hierarchies result in the unequal distribution of resources, with dominant individuals able to monopolise access to food, shelter and reproductive opportunities. However, the short-term benefits of priority access to resources have not always translated into long-term benefits in terms of growth and survival. Here I test whether dominant Atlantic salmon that were able to monopolise a food source in laboratory conditions had a growth advantage over subordinates when returned to their natural stream. High-ranking individuals showed no growth advantage over subordinates over a two-month period. Growth in the wild was also not related to the sex or initial size of individuals, nor the density of other salmon of the same age class within each experimental site. There was, however, variability in growth, with salmon in one site gaining twice as much weight as fish from the other sites. This suggests that resources were limited in availability and that the absence of a relationship between growth and dominance was not due simply to an excess of food being available. The lack of a positive correlation between dominance and growth in the wild may be explained by several mechanisms, including the spatio-temporal variability in resources, inter-specific interactions, disturbance or predation. Although the precise mechanism, or combination of factors, that result in the breakdown of the relationship between dominance and growth is not clear, this study illustrates that dominance status may have negligible effects on growth and fitness in the wild,

which may to a large extent be dependent on other biotic and abiotic factors in addition to competition.

Submitted to Behavioral Ecology

The Shochie Burn

7.2 Introduction

In many competitive environments, stable dominance hierarchies have evolved to the benefit of both dominants and subordinates, since all individuals experience a lower incidence of serious fighting than those in unstable systems (Krebs & Davies 1997). For example, Réale et al. (1996) found that within large groups of feral sheep, rams were unable to develop the stable social bonds that are present within small groups (Rowell & Rowell 1993). This was a major factor in the high level of female mortality induced by sexual harassment during the rutting period because dominant males were unable to deny subordinates access to females (Réale et al. 1996). Dominance relationships are generally thought to result in an unequal distribution of available resources, with a disproportionate amount being monopolised by high-ranking individuals. In the short term, therefore, dominant individuals in many social assemblages are able to gain priority access to resources such as food (e.g. Gill & Thomson 1956; Murton et al. 1966), shelter (e.g. Figler et al. 1999) and mates (e.g. Choe 1994). In the longer term, these advantages are assumed to translate into enhanced growth, survival and reproductive output of dominants relative to subordinates. However, there are conflicting reports on the long-term benefits of dominance for survival and breeding success. For example, dominant red deer hinds produce more surviving offspring over their lives than subordinates (Clutton-Brock et al. 1984, 1986). Social rank has also been shown to be an important determinant of kid production in female mountain goats, although in this case age-specific social rank was not related to the survival of females or their offspring (Côté & Festa-Bianchet 2001). However, dominant individuals do not

always achieve higher reproductive success than their subordinate conspecifics, either because alternative mating strategies, such as sneaky mating, are as successful (Gross 1996), or because there are costs related to high social status that may in fact decrease reproductive success (e.g. Frank et al. 1995; Packer et al. 1995).

There have also been conflicting results with regard to the influence of dominance status on individual growth. For example, juvenile Atlantic salmon of high social rank fed ad libitum from point food sources in laboratory tanks grow at a faster rate than their subordinate conspecifics (Metcalfe et al. 1989; Metcalfe & Thorpe 1992). However, when held in flowing water and fed during restricted times of the day, subordinate fish grow faster than dominants (Huntingford & García de Leániz 1997). When enclosed in shallow fast-flowing "riffle" areas of a natural stream in which availability of food was spatially and temporally variable, there was no correlation between growth and dominance of salmon (Martin-Smith & Armstrong in press). The variation between these studies may be due to dominant fish increasing their foraging advantage sufficiently to compensate for their high rate of energy expenditure (Metcalfe 1986; Cutts et al. 2001) relative to subordinates only when resource distributions are relatively predictable (Martin-Smith & Armstrong in press). In natural pool systems in which resource distribution is highly predictable, there are strong relationships between dominance and growth rates of salmonid fishes (Hughes 1992; Nakano 1995a,b).

There are further mechanisms that may reduce the growth advantage of dominant fish even when food distributions are predictable. Positive correlations between size and dominance were evident among juvenile Atlantic salmon and brown trout when the two species were in allopatry but not when they were living sympatrically (chapter 6). Correlations between dominance and growth may also be exhibited in the absence but not presence of predators (Reinhardt 1999; Reinhardt et al. 2001) and environmental perturbations have been shown to disrupt the stability of dominance hierarchies (Sloman et al. 2001).

Natural streams holding Atlantic salmon often comprise mixtures of habitat types between which the spatio-temporal variability of food supply may differ and in which growth may (e.g. pools) and may not (e.g. riffles) correlate with dominance. Moreover, salmon typically occur with other fish and predators. In view of this range of potential affecting factors the relationship between dominance and growth in the wild is uncertain. Here I report the first test of whether the dominance status of wild juvenile Atlantic salmon, determined by standardised trials in the laboratory, correlates with previous growth and influences their subsequent growth rate and survival when replaced back into their original natural stream.

7.3 Methods

The salmon used in this experiment were caught from the Shochie Burn, a tributary of the River Tay, on July 5th 2000. The fish were captured at an altitude of approximately 200 metres (56°29'N, 3°38'W) where the burn was

approximately 5 metres wide with a predominantly boulder substrate, interspersed with cobble and gravel. The fish population within the burn was dominated by offspring of naturally spawning Atlantic salmon and sea trout, along with resident populations of brown trout. The burn also contained relatively small numbers of eels, lampreys, stone loach, minnows and sticklebacks. All fish receptive to capture by two electrofishing passes within each of six sites were sampled. The sites (dimensions are given in Table 7.1) were separated from each other by at least twenty metres. The lengths and weights of each salmon were measured after each fishing pass. Fish of all species were initially collected in order to obtain an estimate of fish density within each site using the sequential removal method (see Zippin 1958). All but the first ten salmon aged between one and two years old (1+) that were captured at each site were then returned to the downstream end of the site prior to fishing the next site. The ten 1+ salmon, kept for subsequent experimental determination of dominance, represented between 60 and 90% of all 1+ salmon within each site and were placed in holding cages within the stream whilst the other sites were fished. Relocation posts placed at the upstream and downstream ends of each site ensured that fish were returned to the correct location. Experimental fish were transported to the FRS Freshwater Laboratory at Pitlochry in containers of oxygenated water and housed overnight in tangential-flow holding tanks. Fish from each site were kept separate during transport and throughout the laboratory phase of the experiment in order to maintain the integrity of the site data.

Table 7.1. Dimensions of the six sites from which salmon were collected. Each site was measured by taking its length and its width at three points: the midpoint, and the upstream and downstream ends. Area was calculated using the mean of the three width measurements for each site.

		Width (m)			
Site	Length (m)	Downstream	Mid-point	Upstream	Area (m^2)
1	13.4	4.8	4.0	4.2	58.1
2	8.8	4.5	3.7	3.2	33.4
3	10.1	5.2	6.2	5.7	57.6
4	11.6	3.6	3.7	3.9	43.3
5	20.8	5.2	5.7	4.5	106.8
6	11.9	3.5	2.0	4.2	38.5

Fish within each of the six groups were anaesthetised the following morning using benzocaine, weighed, measured and given their own individual alcian blue dye marks on the caudal and dorsal fins for identification in the dominance trials. A passive integrated transponder (PIT) tag was inserted into the peritoneal cavity of each fish so that they could be individually identified on recapture from the wild at the end of the experiment. The fish (fork length = 75.6 ± 0.75 mm (mean ± standard error (S.E.)); weight = 4.67 ± 0.14 g) were then placed in small arenas (one per site) in a flow-through flume system which had glass panels on one side to allow behavioural observations to be made. Each arena measured 50 x 48 cm and had a 3 cm deep layer of gravel substrate and a water depth of 15 cm. The

fish were then left overnight before observations. The following day, food was offered in the form of an individual chironomid released at the upstream end of the testing arena using a pipette. This procedure was repeated at regular intervals throughout the day to allow the fish to acclimatise to the new tank surroundings and feeding technique. This feeding protocol was used in all future dominance trials. Following the day of training, fish were dominance tested over the following six days in a manner identical to that used in chapter 4 (see also Metcalfe et al. 1989). On each day, at 45-minute intervals, a single chironomid was released at the upstream end of each testing arena and the fish scored on their initial position in the tank prior to release of the food item and their ability to compete for it. Ten chironomids were delivered per day in this way and then the scores were added for each fish. Points were awarded as follows:

+1 for holding the most profitable location in the testing arena, defined as the nearest central position downstream of where the chironomids were released,

+1 for obtaining an uncontested food item,

+2 for obtaining the food if the item was contested by another fish.

The individual with the highest overall score on the first day was defined as the most dominant fish in the group, and was removed and placed in the holding tank for that site. If two fish had scores within five points of each other after ten repetitions, then testing continued until the scores differed by five points or more. After removal of the dominant the other fish were fed to excess and left overnight. They were then tested in the same way to find the most dominant of the remaining fish. Dominance testing continued for six days, allowing us to define the six most dominant fish of the ten tested from each site. At the end of the sixth day all fish were returned to the holding tanks. Water temperature

during the dominance trials (measured hourly using a temperature probe placed permanently in the stream tank) ranged from 10.8 to 14.3 °C.

On July 14th 2000 (the day after the dominance trials finished) the salmon were released back into the wild at the downstream end of the site from which they were originally captured. The temperature probe was removed from the stream tank in the laboratory and placed in the stream at the upstream end of the reach from which fish were obtained. Temperature was recorded hourly until fish were recaptured on September 19th 2000, declining from a mean of 16.1 °C in the first week to 11.4 °C in the last (range 7.4 - 23.1 °C). Electrofishing followed a similar procedure to that used when first capturing the fish, with two passes being made between the pegs marking out each site. All fish were collected and measured in order to calculate the density of fish at each site. The recaptured PIT-tagged salmon were then transported to tangential-flow holding tanks at the Almondbank fish hatchery where they were re-weighed and measured on September 21st 2000. Fish were kept in the hatchery to monitor further growth and to investigate the formation of the bimodal distribution (into early and delayed smolting groups) that can arise in salmon parr populations at the beginning of winter (see Thorpe 1977). While in the hatchery the salmon were fed three meals of live chironomid larvae each day for a month and re-weighed and measured on October 25th 2000. Unfortunately, the fish had adapted poorly to hatchery conditions and had lost weight, and so they were sacrificed on October 30th 2000 to determine their sex and retrieve the PIT tags.

7.3.1 Data analysis and statistical treatment

The parameters of greatest interest in this study were the individual changes in growth rate and condition of fish, and the effect that initial rank, size, sex, site and the density of 1+ salmon within each site had on these factors. Only two of the males recaptured showed evidence that they were becoming sexually mature, and there was no obvious indication that these males showed different growth rates or condition than the other recaptured males. Therefore no tests were carried out to determine whether maturity status had any effect on growth and condition. When assessing the influence of rank on growth and condition, individuals were split into three groups according to the rank they achieved in the dominance trials. For each site, the first three individuals removed during the serial removal trials in the laboratory were defined as high-ranking individuals, the next three fish removed were defined as intermediate in rank, whilst fish that remained at the end of the trials were defined as low-ranking individuals.

Specific growth rate (SGR) in terms of weight gained was calculated separately for the period of time in the wild and then in the hatchery for each individual that was recaptured. This was calculated using the formula:

$$SGR_W \text{ (percentage growth per day)} = 100\,[\ln(W_t) - \ln(W_0)] / t$$

where W_0 is the weight at the start date, W_t is the weight at the end date and t is the number of days between the start and end dates. The growth rate of fish in terms of length (SGR_L) was also calculated in the same manner for the period in

the wild. To test for effects of initial size on SGR in the wild and under hatchery conditions, analysis of covariance (ANCOVA) was carried out with SGR (for weight or length) as the dependent variable, and site (fixed factor), size (either initial weight or length) and rank (covariates) being entered into the model with no interaction terms. For both the period spent in the wild and that spent in the hatchery there was no effect of initial weight on SGR_W (wild: $F_{1,25} = 0.18$, $P = 0.674$; hatchery: $F_{1,17} = 0.82$, $P = 0.378$). There was also no effect of initial length on growth in length (SGR_L) in the wild ($F_{1,25} = 0.41$, $P = 0.528$). Therefore the analysis was repeated with the inclusion of the interaction between rank and site, but excluding size as a factor. The effect of within-site density on growth whilst in the wild was determined by comparing the mean SGR for a site with the density of 1+ salmon within that site using Spearman's rank order correlation. To test for an effect of sex on SGR I calculated the deviation of an individual's SGR from the mean for that site, and then performed an independent samples t-test to determine whether these relative growth rates differed for males and females.

The relationship between an individual's length and weight was used as an index of its condition (see Elliott 1984). To test for effects of rank and within-site density on condition, a stepwise multiple regression was carried out with log length as the independent variable and log weight as the dependent variable. Data from all experimental fish were used to test for effects when fish were first captured, whilst only data for recaptured fish could be used to test for effects on recapture. To determine whether fish changed condition during the period in the wild, I used the regression line of log weight against log length on the start date

for all fish that were eventually recaptured as my 'expected' relationship between weight and length. For each recaptured individual I calculated the residual from this line on both the start and recapture date, and compared these using a paired samples t-test. The difference between these two residual values was used as a measure of change in condition. The mean change in condition was then calculated for each rank and sex within each site, and compared using two-way ANOVA with sex and rank as factors. All quoted probabilities are for two-tailed tests of significance.

7.4 Results

There was no significant difference in the overall density of fish between sites, although all sites had a higher density of salmon than of trout (Two-way ANOVA: effect of site: $F_{5,5} = 0.40$, $P = 0.831$; effect of species: $F_{1,5} = 74.50$, $P < 0.001$; Fig. 7.1). In total, 33 out of the original 60 experimental fish were recaptured 76 days after release. All were recaptured in their original sites. Any changes in the within-site densities of 1+ salmon between sampling dates were too small to be detected (paired samples t-test: $t_5 = 1.69$, $P = 0.153$).

There were no significant differences in the lengths and weights of fish of different rank at the start of the experiment (One-way ANOVAs, length: $F_{2,15} = 0.87$, $P = 0.437$; weight: $F_{2,15} = 0.81$, $P = 0.462$). There were also no effects of rank on specific growth rates, either in terms of weight or length, while fish were in the wild (Table 7.2). However, there was a significant effect of site, with fish in site 3 having significantly higher growth rates than fish from other sites (Table

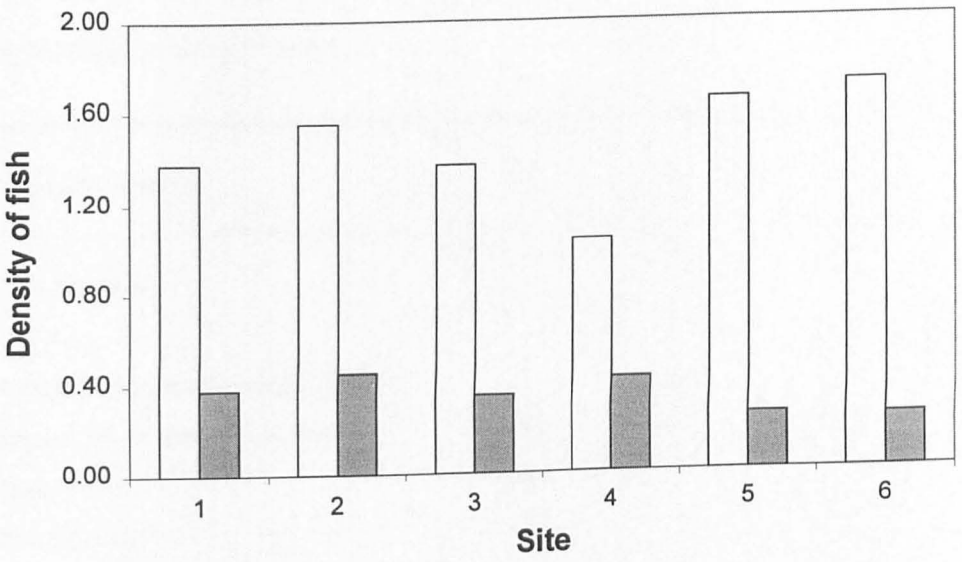


Figure 7.1. Zippin estimates of the density of salmon (open bars) and trout (shaded bars) of all age classes per square metre in each site.

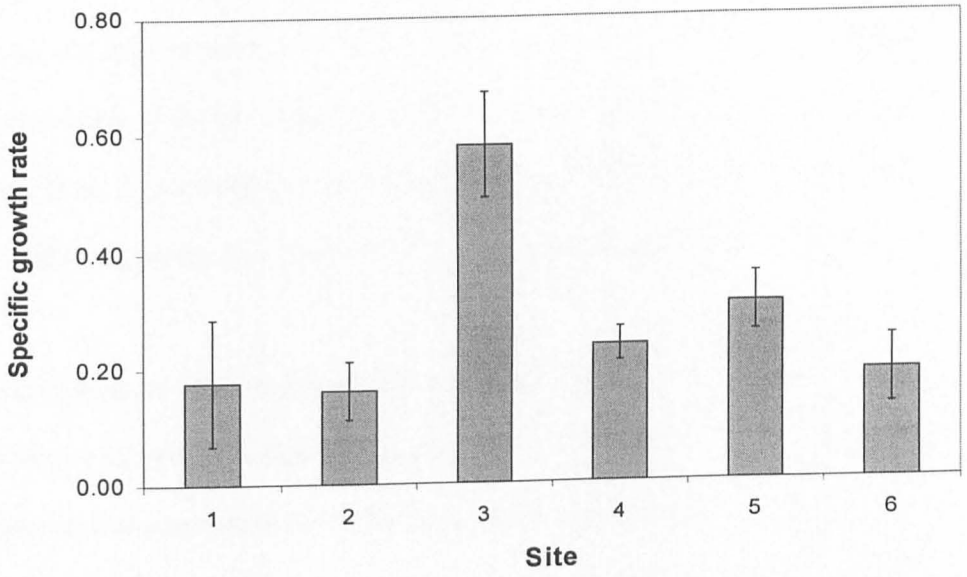
Table 7.2. Summary of results from analyses of covariance to determine the influence of site (factor) and rank (covariate) on a) specific growth rates in terms of both weight and length in the wild and b) specific growth rate in terms of weight under hatchery conditions.

Source of variation	d.f.	F	P
a) In the wild			
Growth in terms of weight change			
Comparison of regression slopes	5,21	0.53	0.751
Effect of site	5,26	6.35	0.001
Effect of rank	1,26	2.13	0.156
Growth in terms of length			
Comparison of regression slopes	5,21	0.47	0.792
Effect of site	5,26	9.06	< 0.001
Effect of rank	1,26	0.39	0.536
b) In the hatchery			
Growth in terms of weight change			
Comparison of regression slopes	4,14	0.66	0.628
Effect of site	5,18	2.36	0.082
Effect of rank	1,18	5.62	0.029

7.2; Fig. 7.2). This site effect was not related to the initial density of 1+ salmon as there was no significant relationship between within-site density and growth rate, either in terms of length (Spearman rank order correlation: $r_s = -0.319$, d.f. = 6, $P = 0.538$), or weight ($r_s = -0.261$, d.f. = 6, $P = 0.618$). The sex of fish had no impact on their rank ($\chi^2 = 0.16$, d.f. = 2, $P = 0.924$) or on their growth rate in the wild (independent samples t-test: $t_{26} = 1.35$, $P = 0.188$). However, there was a trend for females to grow faster in terms of length than males (independent samples t-test: $t_{26} = 1.99$, $P = 0.057$).

At the time of initial capture log weight was closely related to log length of the fish ($r^2 = 0.960$, $F_{1,58} = 1416.7$, $P < 0.001$), but stepwise multiple regression showed that rank and the density of 1+ salmon within each site did not explain any of the residual variation in weight for a given length (i.e. body condition). They similarly were not entered as significant variables in the equivalent multiple regression predicting log weight at the time of recapture (effect of log length: $r^2 = 0.944$, $F_{1,31} = 542.7$, $P < 0.001$). However, the condition of experimental fish did change whilst they were in the river, with the majority of fish getting thinner relative to their length (paired samples t-test on relative condition at start and end of period: $t_{32} = 8.15$, $P < 0.001$). There was no effect of sex or rank on this change in condition (Two-way ANOVA: effect of sex, $F_{1,15} = 0.20$, $P = 0.665$; effect of rank, $F_{2,15} = 3.30$, $P = 0.065$), although there was a trend for fish of high rank to lose more weight relative to their length than lower ranked fish.

a)



b)

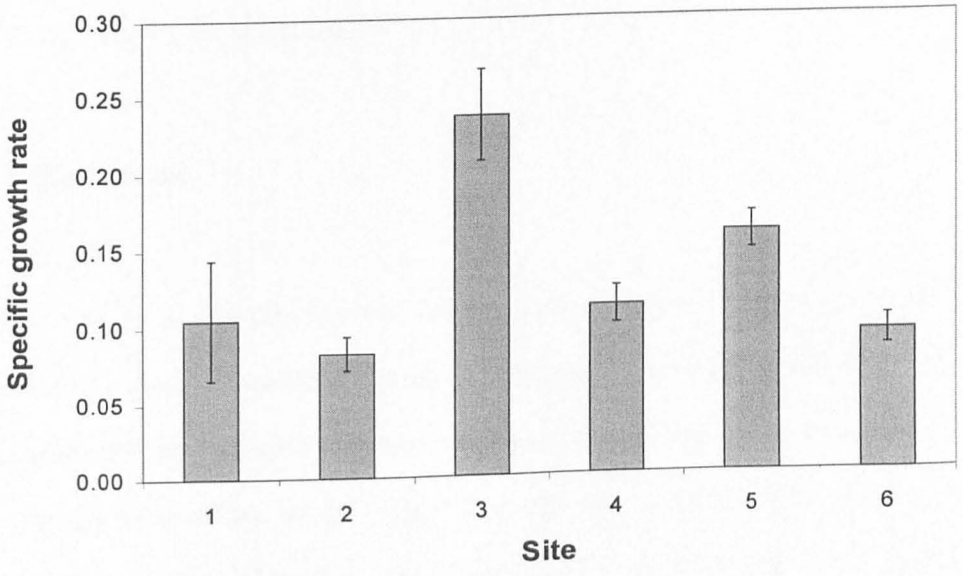


Figure 7.2. Specific growth rates in the stream over the period from initial capture to recapture for fish from different sites in terms of a) weight and b) length.

There was no significant effect of rank, initial length or site on the probability of recapturing fish (logistic regression: effect of rank, $R_{1,7} = 0.95$, $P = 0.330$; effect of length, $R_{1,7} = 0.02$, $P = 0.903$; effect of site, $R_{5,7} = 3.03$, $P = 0.695$). Examination of the size distributions of fish on the initial capture and recapture dates (Fig. 7.3) reveals that the bimodal distribution associated with migration the following spring (see Thorpe 1977) had not developed in this population.

Although all fish lost weight under hatchery conditions, there was a significant difference in rates of weight change between fish of different ranks, with fish of lower rank losing weight at a faster rate than those of high rank (Table 7.2; Fig. 7.4). There was no effect of capture site on the rates of weight change of fish under hatchery conditions (Table 7.2), and no relationship between the growth rate of individuals in the wild and their growth rate in the hatchery (regression: $r^2 = 0.048$, $F_{1,23} = 1.15$, $P = 0.294$).

7.5 Discussion

There was no relationship between size and rank at the start of the experiment when fish were removed from the wild. Furthermore, the rank that fish achieved in dominance tests within the laboratory had no effect on their subsequent growth or change of condition in the wild. Although the bimodal distribution that separates early- and delayed migrants (Thorpe 1977) had not formed by the time the fish were sacrificed, it is unlikely that the rank achieved in dominance trials would have greatly affected which mode an individual entered, as there was no effect on growth in the wild.

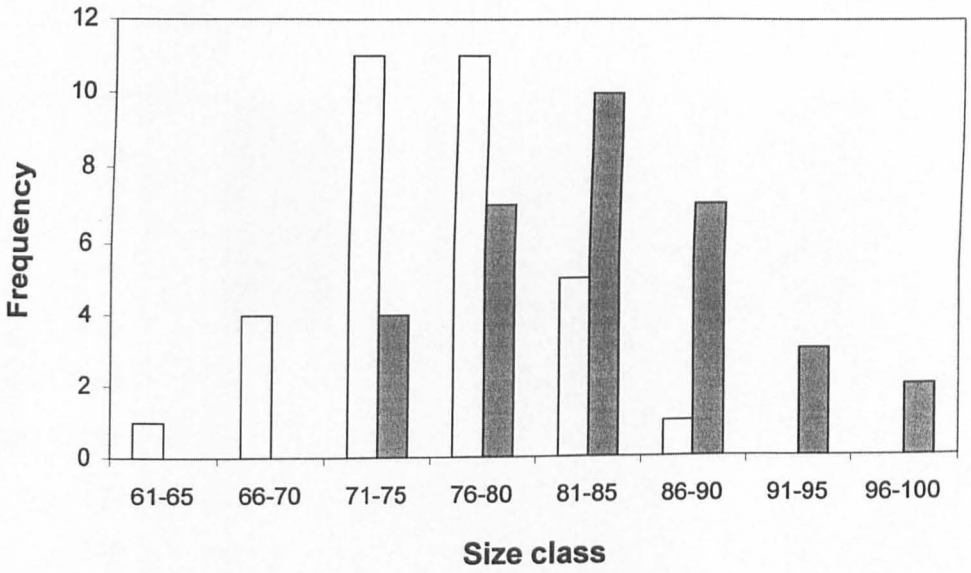


Figure 7.3. Size distribution of recaptured fish on initial capture (open bars) and recapture (shaded bars) dates.

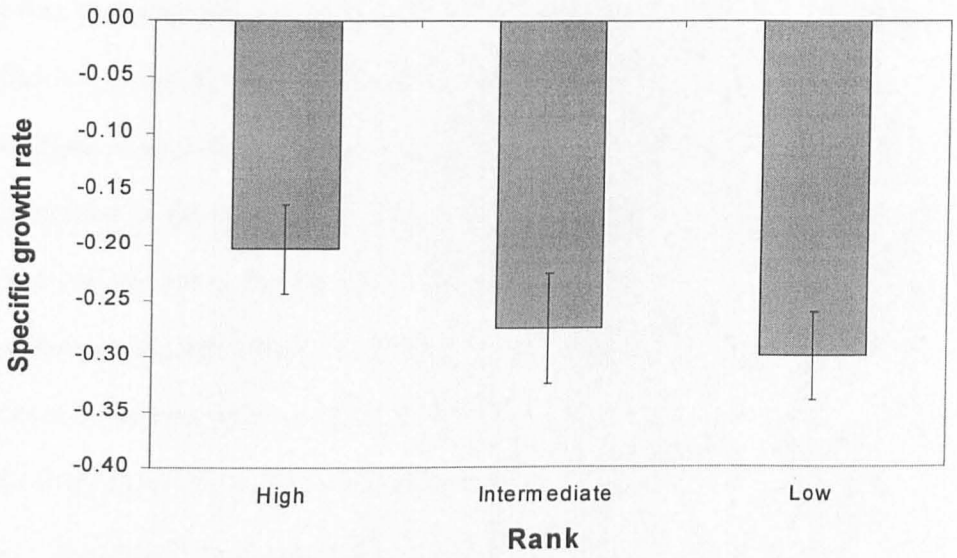


Figure 7.4. Specific growth rates in terms of weight for recaptured fish of different rank whilst kept under hatchery conditions. Note that values are negative since fish were losing weight.

The lack of correlation between rank and growth in the wild is in contrast to laboratory studies of juvenile salmonids in which dominant individuals have been able to monopolise positions that afford maximum potential profit and thus achieve higher growth rates (e.g. Fausch 1984; Metcalfe et al. 1990b). Dominant individuals in this study did relatively better than subordinates in hatchery conditions where they lost less weight, but had no growth advantage over subordinates in the wild. Social status within the laboratory has been shown to play a critical role in the life history of Atlantic salmon reared under hatchery conditions, with individuals of high rank undergoing the transformation to the seaward migration phase of the life cycle a year earlier than lower ranked individuals (Metcalfe & Thorpe 1992; Thorpe et al. 1998). However, dominance status has not been linked with growth in all laboratory studies of fish (Huntingford & García de Leániz 1997; Cutts et al. 2001). For example, while Cutts et al. (2001) found positive relationships between aggression, metabolic rate and number of feeding attempts in groups of Arctic charr, there was no relationship between competitive ability and subsequent growth. The lack of a relationship between number of feeding attempts and growth was interpreted as a cost of dominance, with individuals that obtained more food only doing so through increased effort (Cutts et al. 2001).

High ranking individuals may incur costs associated with aggression, either in terms of the energy expended during territorial defence or the loss of feeding opportunities whilst involved in territorial aggression (Elliott 1990; Adams et al. 1998; chapter 6). Moreover, basal metabolic costs correlate positively with dominance (Metcalfe et al. 1995). The costs of dominance and aggression can be

outweighed by the benefits of resource defence when food is spatially defensible, giving rise to a positive relationship between dominance and growth (Fausch 1984; Hughes 1992; Nakano 1995a,b). However, when the spatio-temporal distribution of food is more unpredictable the costs and benefits of dominance may become balanced, with dominant individuals receiving no growth benefits (Martin-Smith & Armstrong in press). The predictability of resources is therefore one factor that may disrupt the relationship between dominance and growth. Grand & Grant (1994) highlighted the importance of resource variability in determining the effectiveness of feeding strategies. They found that in groups of juvenile convict cichlids resource defence was the most effective strategy when food was spatially predictable, but when the distribution of food became unpredictable exploitative competition, via scrambling, became a more successful strategy. In predictable environments in the laboratory (Hughes 1992) and in the headwaters of natural pools (Nakano 1995a,b) dominant salmonids have been able to defend the best feeding sites and hence have grown faster than subordinates have. However, dominant individuals that had been able to monopolise point sources of food showed no growth benefits over subordinates in spatially and temporally less predictable conditions in natural streams (Martin-Smith & Armstrong in press; this study). Therefore, although dominants may be able to monopolise resources in riffle habitats in the wild these are not necessarily the most profitable (see Bachman 1984) and any benefits gained by tracking high quality patches may be countered by the costs of dominance (Martin-Smith & Armstrong in press).

The patchy nature of the resources experienced by fish in this experiment is highlighted by the variability in growth rates observed. Fish from one site gained twice as much weight as fish from the remaining sites, and this variability was not related to the density of 1+ salmon within each site. This disparity in growth between the sites suggests that the growth rates of the majority of 1+ salmon in the stream were limited by the availability of resources. Therefore, the absence of a relationship between growth and dominance was not due simply to an excess of food being available.

The stretch of stream used in this experiment consisted of riffle, where the distribution of food is spatially and temporally unpredictable (Martin-Smith & Armstrong in press), and pools, where the food distribution is more predictable and defensible (Nakano *et al.* 1999). Therefore, unlike Martin-Smith & Armstrong (in press), salmon in this study had access to more predictable resources than those available in riffles, and yet there was no evidence that dominant individuals were able to gain an advantage over subordinate salmon in food acquisition. This may be related to the presence of brown trout that are known to dominate salmon in competition for resources (Kalleberg 1958; Kennedy & Strange 1986a,b; chapter 2). Trout may have monopolised the predictable food resources in the headwaters of pools and thus denied dominant salmon access to these defensible areas. Sympatric association of salmon and trout has recently been shown to affect within-species dominance hierarchies in stream channels with the correlation between size and dominance that is present in allopatric groups not being present in sympatric groups (chapter 6). Chapter 6 shows that resource partitioning and a non-aggressive feeding strategy adopted

by some salmon may disrupt the positive relationship between size and dominance, and similar behaviour may be a factor in explaining the lack of such a relationship in this study.

Variable environmental conditions may affect the strength of social hierarchies and determine whether dominance status is associated with growth. Frequently occurring environmental perturbations, such as spates and droughts, could alter the strength of social hierarchies in the wild. Sloman et al. (2001) showed that a stable hierarchy of brown trout broke down after a rapid dewatering event in laboratory tanks. Consequently, they suggest that hierarchies may not form in small streams which experience large fluctuations in water level, unlike in large rivers where environmental conditions are more stable (see Bachman 1984). However, it may be difficult to extrapolate results from laboratory experiments to natural streams as the effects of water level manipulations vary between artificial and near-natural conditions (see Armstrong et al. 1998; Huntingford et al. 1998). Furthermore, if the proposed breakdown in social hierarchy (see Sloman et al. 2001) had occurred in my study then one would expect a negative relationship between dominance and growth, since dominant individuals have been shown to have higher metabolic rates (Metcalfe et al. 1995; Cutts et al. 2001).

The level of predation within a system can also play a role in determining the growth rates of dominant and subordinate fish. Reinhardt (1999) found that in the absence of predation risk in simulated natural conditions larger coho salmon fry monopolised the most profitable feeding sites and therefore grew better than relatively smaller fish. However, the level of agonistic behaviour was reduced

under simulated predation risk thus allowing smaller fish, which were apparently more willing to forage under high predation pressure (Reinhardt & Healey 1999), to gain access to the most profitable feeding sites and grow relatively faster. Similarly, Reinhardt et al. (2001) found that the largest individuals in groups of masu salmon released into stream enclosures grew better than smaller fish in the absence of predators, but not in the presence of the predaceous Japanese huchen. These studies suggest that predation risk leads to a decrease in interference competition between individuals thus providing a relative advantage to smaller fish in comparison to situations where predation risk is low (see Reinhardt et al. 2001).

The evidence suggests therefore that one or more of the mechanisms associated with spatio-temporal resource variability, sympatric interactions, disturbance and predation may have resulted in the competitive advantages under laboratory conditions not translating into higher growth rates in the wild. The behaviour of individuals within social hierarchies in the wild has previously been shown to change in response to environmental conditions (e.g. Nakano et al. 1999; see also Dunson & Travis 1991 and references therein). Nakano et al. (1999) found that a drop in the abundance of drifting prey for which Dolly Varden and white-spotted charr compete in Japanese streams, forced the competitively inferior Dolly Varden to shift to benthic foraging. This study shows that although wild fish establish dominance hierarchies that are evident in stream enclosures (Martin-Smith & Armstrong in press) and under laboratory conditions (Metcalfe et al. 1989; Metcalfe & Thorpe 1992; this study), the influence that dominance status

has on growth and fitness in the wild may be negligible and to a large extent dependent on other biotic and abiotic factors in addition to competition.

CHAPTER 8: GENERAL DISCUSSION

8.1 Introduction

The overall aim of this thesis was to examine intra- and inter-specific competition among juvenile Atlantic salmon and brown trout. This study focused on two critical times, the period from shortly after emergence until later in the first summer when mortality is at its peak (Elliott 1989; Giles 1994), and winter, during which there can be a bottleneck for some salmonid populations (Bjornn 1971; Mason 1976). In addition, the stability of dominance hierarchies and their effects on growth and survival in the wild were studied on older individuals during the summer. I have demonstrated that Atlantic salmon and brown trout compete for foraging (chapter 2) and sheltering (chapter 3) habitats during winter, thus illustrating that competition between the two species is not restricted to the summer months. The acquisition of resources, whether in terms of food or habitat, has been shown to be influenced by dominance status (chapters 2, 4 and 6) and prior residence (chapters 3 and 4). However, the influence of these factors on resource acquisition has been shown to depend on environmental conditions, such as the species assemblage (chapter 6) and the predictability of the resource (chapters 5 and 7).

8.2 Competition during winter

It has been known for some time that juvenile salmonids undergo a shift in activity from being predominantly diurnal in the summer, to being primarily

nocturnal during the winter (Fraser et al. 1993, 1995). To facilitate prey capture, this shift in activity is associated with a preference for slow-flowing water at night in brown trout (Mäki-Petäys et al. 1997), brook trout (Cunjak & Power 1986), rainbow trout (Riehle & Griffith 1993) and coho salmon (Nickelson et al. 1992). This thesis has shown that Atlantic salmon have a similar preference for slow-flowing water (chapter 2; see also Whalen & Parrish 1999) and that salmon compete with brown trout for this foraging habitat. During the day in winter salmonids shelter in interstitial spaces in the substrate or under overhanging banks (Bustard & Narver 1975a,b; Cunjak 1988; Heggenes & Saltveit 1990). The availability of such refuges has been shown to be both limiting and critical for salmonid survival (Hillman et al. 1987; Griffith & Smith 1993). However, only Gregory & Griffith (1996b), in their study of rainbow trout, have quantified the level of competition for daytime shelters between juvenile salmonids. This study therefore provides the first record of aggression between species for sheltering habitat during winter, and shows that intra- and inter-specific competition for refuges can be equal in intensity (chapter 3).

Previous reports of competition between Atlantic salmon and brown trout have been confined to the summer months (e.g. Kennedy & Strange 1980, 1986a,b). This thesis shows that Atlantic salmon and brown trout continue to compete for food and habitat during the winter months. Furthermore, evidence from other studies suggests that this competition may be more critical to the survival of salmonids than competition during the summer months. Several studies have suggested that the limited availability of slow-flowing water or cobble-boulder substrate in which fish can hide may play a crucial role in the numbers of

salmonids and other freshwater fish that streams can support (Nickelson et al. 1992; Cunjak 1996; Whalen & Parrish 1999; Solazzi et al. 2000). The impact that habitat limitations may have on overwintering salmonids may be further increased by the fact that whilst different age groups of fish use different habitats during summer (Kennedy & Strange 1982), they use similar habitats during winter (Whalen & Parrish 1999). It would be very interesting therefore to conduct comparative studies on the growth and survival of over-wintering salmon and trout in the wild under different levels of intra- and inter-specific competition. Although such studies invariably involve problems associated with variable environmental conditions between rivers, or between sections of the same river, similar work has already shown the importance of habitat enhancement both in terms of slow-flowing water (Solazzi et al. 2000) and cobble-boulder substrate (Hillman et al. 1987). Should competition within or between species affect the survival of overwintering salmonids then it could have important implications for management strategies, and these will be considered in more detail below.

8.3 Resource acquisition

Dominance rank and prior residence advantage have been associated with successful resource acquisition within many animal groups including salmonids. Dominance status has been shown to be influential in determining growth rates and subsequent life-history strategies in salmon (e.g. Metcalfe et al. 1989) and prior residence has been found to have an important influence on which fish become dominant (e.g. Glova & Field-Dodgson 1995; Rhodes & Quinn 1998;

Cutts et al. 1999a,b). It is unsurprising therefore that I found dominance rank (chapters 2, 4 and 6) and prior residence advantage (chapters 3 and 4) to play an important role in the acquisition of food and habitat. However, the interaction between these two factors within salmonids has only been studied in Atlantic salmon parr (Huntingford & García de Leániz 1997) and not when fry are first establishing territories, which is perhaps the most important time of territory acquisition. Chapter 4 examined the relative influence of intrinsic dominance status and prior residence on food acquisition in Atlantic salmon fry and demonstrated that their effects were additive, independent and approximately equal in strength. However, this thesis also shows that the importance of dominance status (chapters 6 & 7) and prior residence (chapters 4 & 5) are not constant.

Most experimental investigations of the impact of social status do so within the atypical situation of a single isolated species. By examining social dominance within sympatric as well as allopatric populations of brown trout and salmon I demonstrated that the advantages of social dominance are dependent on the composition of the species assemblage in which an individual lives (chapter 6). Furthermore, the ability to monopolise a point food source does not necessarily translate into growth benefits in the wild (chapter 7; see also Martin-Smith & Armstrong in press). There are a range of factors, such as spatio-temporal variability in food supply, disturbance, predation (see chapter 7) or sympatric associations (chapter 6) which may cause the relationship between dominance status and growth to break down. However, the positive relationship between dominance and growth in natural pool habitats (Nakano et al. 1999) where the

food resource is more predictable than on riffles suggests that the predictability in food supply is a main factor. The distribution of food has been found to be a key factor in determining the strength of social hierarchies in other species. Pruetz & Isbell (2000) found that when food was spatially dispersed vervet and patas monkeys exhibited relatively weak, non-linear dominance hierarchies but when vervet monkeys switched habitats and fed on spatially clumped resources they exhibited a stronger, linear dominance hierarchy (see also Ruzzante 1994). Prior residence was also shown to provide an advantage to Atlantic salmon fry under certain conditions (chapter 4) but not others (chapter 5). Once again this may be related to the value and predictability of the resource, with advantages gained through intrinsic dominance status or prior residence being expressed to a greater degree when the value of the resource is high (see Clutton-Brock et al. 1979; Verrell 1986; Haley 1994; Nijman & Heuts 2000).

The findings of this thesis warrant further investigation, under as natural conditions as possible, in order to ascertain the importance of dominance and prior residence to individual salmon and trout in the wild. For example, it would be interesting to determine the long-term effects of intrinsic status and prior residence on growth of Atlantic salmon fry under more natural conditions. The problem with working with fry in semi-natural flume systems is the difficulty of observing the behaviour of small fry in artificial streams that provide natural camouflage. However, if this problem could be overcome then food could be delivered in an unpredictable but more natural manner than was possible in chapters 4 and 5. Considering that predation risk (Reinhardt 1999; Reinhardt et al. 2001) and the species assemblage (chapter 6) can also affect the formation of

hierarchies it would also be interesting to determine what effect, if any, trout fry and the threat of predation would have on the growth and territorial behaviour of Atlantic salmon fry. In addition, the effect that the presence of older year classes had on behaviour within age classes could be examined. This may be particularly important during the winter when different age classes show similar habitat preferences (Whalen & Parrish 1999). The importance of studying these interactions is highlighted by Bryant & Newton (1996), who found that the relationship between dominance and survival of dippers in the wild was apparently different between age classes and sexes. Bryant & Newton (1996) also stress the significance of experimental design. For instance, if dominance interactions in the wild occur between members of both sexes and all age classes of a species then it may be inappropriate to study the formation of hierarchies within only one age class or sex. Similarly, if two closely related species coexist in the wild it may be necessary to study social hierarchies in mixed groups (chapter 6).

8.4 Resource partitioning

This thesis has shown that Atlantic salmon and brown trout compete for habitat (chapters 2 & 3) and food (chapter 6) resources. However, they coexist alongside each other in the wild without one or the other becoming extinct. As mentioned in the introduction (chapter 1), this coexistence is made possible by ecological segregation, or the partitioning of available resources. This thesis has witnessed resource partitioning between species in terms of space use (chapters 2 & 6) and within species in terms of time of day (chapter 6). Atlantic salmon and

brown trout were observed to adopt different positions in the water column both whilst active during the night in winter (chapter 2) and during the day in summer (chapter 6), with salmon resting on the substrate and trout holding position in the water column. Bremset & Berg (1999) witnessed a similar segregation of salmon and trout in the wild that allows them to utilise similar microhabitats at the same time. The partitioning of resources can also be achieved in time, as witnessed in chapter 6 where dominant and subordinate trout fed at different times of the day (see also Alanärä & Brännäs 1997; Alanärä et al. 2001). When salmon and trout coexisted there were lower levels of severe aggression than when each species was in allopatry (chapter 6). This reduced level of harmful aggression raises an interesting question: would long-term growth be higher in sympatric groups of salmon and trout than in allopatric groups because of the lower level of energy expended on aggression? Kennedy & Strange (1986a) found that Atlantic salmon grew more slowly in stream reaches containing brown trout than in those without trout. However, the lack of replication and the fact that the total biomass of fish varied between stream reaches means it would be interesting to conduct long-term trials of a more controlled nature. Indeed, contrasting results have been found in relation to the growth of salmonids in mono- and duoculture within aquaculture. Mork (1982) and Holm (1989) found that raising salmonids in duoculture improved growth rates, whilst Jobling et al. (1998) found negative effects on salmon growth when rearing them with brown trout as opposed to other salmon. If a difference was found in the growth rates of salmon and trout under conditions of allopatry and sympatry then it would have implications for management and stocking strategies, regardless of whether there was a positive or negative effect on growth. An alternative measure for

evaluating the success of salmon and trout under conditions of allopatry and sympatry would be the total biomass of fish of a given size that a stream could support.

8.5 Implications for fisheries management and aquaculture

The results reported in this thesis are of value for those involved in the management of natural streams and the aquaculture industry. This is because a better understanding of the natural behaviour of salmon and trout is essential in both applied situations. Experiments were conducted in arenas appropriate for making detailed observations of behavioural interactions among fish and in some cases the next stage will be to test the findings under conditions more closely matching those of natural streams or fish farming as appropriate. Chapter 7 demonstrated the value and importance of using field studies to test inferences derived from laboratory observations in an ecological context.

The importance of slow-flowing water (chapter 2) and streambed refuges (chapter 3) to overwintering salmonids is consistent with the results of habitat enhancement programs (Hillman et al. 1987; Solazzi et al. 2000). Whilst the provision of these habitats is therefore essential for salmonid recovery programs this thesis highlights that intra- and inter-specific competition for these resources may be intense. Therefore, management strategies will have to consider not only the species of interest but also the nature and density of fish populations already present within the system. Moreover, it raises the possibility that habitat enhancements that increase populations of both salmon and trout in the summer

may result in reduced numbers of salmon smolts due to competition between the species during winter.

This thesis shows that whilst certain dominant individuals are able to monopolise a point source of food in the laboratory this does not necessarily translate into improved growth in the wild (chapter 7). The predictability of the food resource may play an important role in the break down of the relationship between dominance and growth. If this proves to be the case then this may be used to improve feeding techniques in aquaculture. Noakes & Grant (1992) suggest that food should be delivered in an indefensible manner, by providing food randomly either in space or time, in order to obtain more uniform growth rates. The findings of this thesis support this proposal, which may be important as recent evidence suggests that social suppression of growth does occur at aquaculture densities (K.F. Cubitt et al. unpublished data).

The natural sheltering behaviour of salmonids during winter has led to the suggestion that growth rates of fish may be improved with the provision of shelter to fish in aquaculture, particularly if food was delivered to the shelter (Valdimarsson 1997). Shelters have indeed been shown to be beneficial in the crayfish farming industry where they reduce levels of mortality by intra- and inter-specific predation (Figler et al. 1999). However, this study suggests that competition may occur for any shelter that was provided (chapter 3). Therefore, shelter provision may actually create more conflict rather than reducing aggression between individuals, although hatchery-reared individuals have been shown to share shelters more frequently than wild fish (Griffiths & Armstrong in

press). Commercially cultured fish may therefore be able to gain growth benefits from shelter use without suffering the costs of competition for shelter (Griffiths & Armstrong in press).

8.6 Conclusions

This thesis has studied the formation of within-species hierarchies and underlined the importance of aggressiveness in determining status in groups of salmon and trout. However, the complexity of hierarchy formation is shown to be influenced by inter-specific interactions, environment, season and the nature of the resource for which individuals are competing. Future work should address these issues on a larger scale, or ideally in the wild, where there is a lack of replicated studies examining inter-specific competition between Atlantic salmon and brown trout, and indeed other salmonid species (Fausch 1998). The potential ecological and fitness consequences of coexistence have been studied using reciprocal removal experiments in Orange-crowned and Virginia's warblers (Martin & Martin 2001a,b). These studies have revealed that the behaviourally subordinate Virginia's warblers have similar reproductive success in sympatric and allopatric habitats (Martin & Martin 2001b), despite having increased reproductive success in sympatric habitat when Orange-crowned warblers were experimentally removed (Martin & Martin 2001a). The apparent discrepancy between the results may be related to density changes associated with removal experiments (Fausch 1998), however, such experiments still allow us to address certain important questions. For example, do individuals in removal plots experience reduced costs, or shift their patterns of resource use towards those of the opposite

species, when compared to conspecific individuals in control plots? The influence that such interspecific interactions, as well as environmental and seasonal variability, have on growth in salmonid species in the wild is a very interesting topic that warrants further investigation. The results of this thesis and the widespread nature of sympatric associations in the natural world suggest that such studies could provide valuable insights into competition in a far wider context than salmonids.

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APPENDIX 1

Common name	Scientific name	Chapter
Polychaeta:		
Sedentary polychaete	*Serpula vermicularis*	3
Insecta:		
Mayfly	*Baetis* sp.	2
Paper wasp	*Polistes* sp.	1,6
Tropical butterfly	*Hypolimnas bolina*	5
Crustacea:		
Common shrimp	*Palaemon elegans*	4
Red swamp crayfish	*Procambarus clarkii*	1,3
White river crayfish	*Procambarus zonangulus*	3
Stone crayfish	*Austropotamobius torrentium*	3
Signal crayfish	*Pacifastacus leniusculus*	3
Poli's stellate barnacle	*Chthamalus stellatus*	1
An acorn barnacle	*Balanus balanoides*	1
Amphibia:		
Dart poison frog	*Dendrobates pumilio*	1,4
Green frog	*Rana clamitans*	4
Harlequin frog	*Atelopus varius*	4
Bullfrog	*Rana catesbeiana*	4
Pisces:		
Salmonidae:		
Atlantic salmon	*Salmo salar*	1-8
Brown trout	*Salmo trutta*	1-8
Rainbow trout	*Oncorhynchus mykiss*	2,3,6,8
Arctic charr	*Salvelinus alpinus*	2,6,7

Coho salmon	*Oncorhynchus kisutch*	2,3,6,7,8
Cutthroat trout	*Oncorhynchus clarki*	3,6
Chinook salmon	*Oncorhynchus tshawytscha*	3
Arctic grayling	*Thymallus arcticus*	1
Brook charr	*Salvelinus fontinalis*	6,8
Dolly Varden	*Salvelinus malma*	6,7
White-spotted charr	*Salvelinus leucomaenis*	6,7
Masu salmon	*Oncorhynchus masou*	7
Others:		
Green swordtail fish	*Xiphophorus helleri*	1,4
Convict cichlid	*Cichlasoma nigrofasciatum*	4,7
Freshwater angelfish	*Pterophyllum scalare*	1,4,5
Mouth breeding cichlid	*Oreochromis mossambicus*	4,5
Three-spine stickleback	*Gasterosteus aculeatus*	1,7
Eel	*Anguilla anguilla*	7
Lamprey	*Lampetra* sp.	7
Stone loach	*Noemacheilus barbatulus*	7
Minnow	*Phoxinus phoxinus*	7
Japanese huchen	*Hucho perryi*	7
Aves:		
Willow tit	*Parus montanus*	1,4
European robin	*Erithacus rubecula*	4
Marsh tit	*Parus palustris*	4
Blue tit	*Parus caerulus*	1
Great tit	*Parus major*	1
White-throated sparrow	*Zonotrichia albicollis*	5
Dipper	*Cinclus cinclus*	8
Orange-crowned warbler	*Vermivora celata*	8
Virginia warbler	*Vermivora virginiae*	8
Mammalia:		
Highveld mole-rat	*Cryptomys hottentotus pretoriae*	1
Northern elephant seal	*Mirounga angustirostris*	5

Sheep	*Ovis aries*	7
Red deer	*Cervus elaphus*	7
Mountain goat	*Oreamnos americanus*	7
Vervet monkey	*Chlorocebus aethiops*	8
Patas monkey	*Erythrocebus patas*	8

Maintenant, je vais skier!!